The Neoptera of the key-Lagerstätte Hagen-Vorhalle

Paleo-environmental history, taphonomy, systematics, and the exploration of new Lagerstätten

Doctoral Thesis
(Dissertation)

to be awarded the degree

Doctor rerum naturalium (Dr. rer. nat.)

submitted by

Dipl.-Geol. Jan-Michael Ilger

from Osnabrück (Germany).

Approved by the Faculty of Energy and Management Science,
Clausthal University of Technology.

Date of oral examination:
December 15, 2011

Chairperson of the Board of Examiners

Prof. Dr.-Ing. Norbert Meyer

Chief Reviewer

Prof. Dr. rer. nat. Carsten Brauckmann

Reviewer

Prof. Dr. rer. nat. Hans-Jürgen Gursky

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2011

Preface

This doctoral thesis (Dissertation) is based on the scientific output resulting from a promoted DFG project (BR 1253/4-1) and its extended application (BR 1253/4-2) with the following title: "The Paoliidae and their significance for the basal phylogeny of the Pterygota".

The present project is estimated to end in May 2012. Its final phase will be sustained in close cooperation with the paleoentomological research group of the Charles Universtiy in Prague (Czech Republic). New findings from the Upper Silesian Basin of the Czech Republic and Poland will enable extensive comparisons with the material from Hagen-Vorhalle and Fröndenberg.

The nomenclature of the taxa follows the set of rules of the 4th edition of the International Code of Zoological Nomenclature produced by the International Commission on Zoological Nomenclature (RIDE et al. (1999); ICZN). In citations of authorship of taxa there is always a comma between author(s) and year of publication to distinguish it from other quotes from literature. For example: *Kemperala hagenensis* BRAUCKMANN, 1985. If there are more than two authors, they are abbreviated with "et al.". Synonymy lists follow international standards as summarized e.g. by MATTHEWS (1973).

This thesis refers to a large number of botanical and zoological taxa, both Recent and Fossil. If all of these taxa were cited, there would be an inflationary swelling of the list of references. Therefore the author decided to exclusively account for invertebrate taxa in this context. For vertebrate taxa authorships and the year of publication are given in the text but they do not occur in the reference list. Authorships of (paleo-)botanical, "algae," and unicellular taxa are not considered in the text and reference list.

Stratigraphical nomenclature follows in general the standards of the German Stratigaphic Commission (DEUTSCHE STRATIGRAPHISCHE KOMMISSION (2002); DSK) and the ICS (INTERNATIONAL COMMISSION ON STRATIGRAPHY 2009). In names of periods, epochs, ages etc. the English ending "-ian" is preferred instead of German (Latin) "-ium", this is also the case for terms that describe a local German stratigraphic segment. In the case of doubt the spelling recommended by the ICS is preferred. For example: Westphalian instead of Westfalian or Westfalium.

The terms "early," "middle," and "late" are consequently used to name sub-divisions of geological periods. Terms like "lower" and "upper" are avoided. For example: Late Carboniferous instead of Upper Carboniferous for the Pennsylvanian. These adjectives are strictly capitalized. In the case of a more precise sub-division the additional adjective is always uncapitalized. For example: early Late Carboniferous.

Acknowledgments

The author gratefully thanks his doctoral supervisor Prof. Dr. C. Brauckmann (Clausthal-Zellerfeld; Germany) for his encouragement, intensive support, willingness for controversial discussion, and assistance in literature search. The co-referee Prof. Dr. H.-J. Gursky (Clausthal-Zellerfeld) is warmly thanked for his review and supportive comments. Furthermore Prof. Dr. M.S. Engel (Lawrence, KS; USA) is thanked for rendering an expert opinion on the thesis.

To permit a financial support by the DFG and much assistance to write the first and extended application the author wants to express gratitude to Prof. Dr. J.W. Schneider (Freiberg; Germany), Prof. Dr. J. Rust (Bonn; Germany), and Dr. E. Gröning (Clausthal-Zellerfeld).

For linguistic corrections on the English manuscript and elimination of his German pseudo-anglicisms the author thanks especially Dr. R.J. Beckemeyer (Wichita, KS; USA), Dr. J. Dunlop (Berlin; Germany), and Dr. C.-D. Sattler (Clausthal-Zellerfeld). Dr. D. Shcherbakov (Moscow; Russia) is thanked for his Russian language support.

The following persons (in alphabetical order) are thanked for their approaches and providing literature—and sometimes even for excitation and motivation: Dr. R.J. Beckemeyer, Prof. Dr. W. van Berk, (Clausthal-Zellerfeld), Dr. O. Béthoux (Freiberg), Dr. L. Feldmann (Benningen am Neckar; Germany). Dr. O.F. Gallego (Corrientes; Argentina), Dr. D. Grzegorczyk (Münster; Germany), Dr. N. Hauschke (Halle (Saale); Germany), T. Hegna (New Haven, CT; USA), Dr. K.J. Herd (Odenthal-Holz; Germany), Dr. T. Hörnschemeyer (Göttingen; Germany), Dr. E. Jarzembowski (Kent; UK), Prof. Dr. K.-D. Klass (Dresden; Germany), Prof. Dr. O. Kraus (Hamburg; Germany), Dr. E. Krzemińska and Dr. W. Krzemiński (both Kraków; Poland), Prof. Dr. J. Kukalová-Peck (Ottawa; Kanada), Prof. Dr. R.G. Martins-Neto † (Juazeiro do Norte; Brazil), Prof. Dr.-Ing. N. Meyer (Clausthal-Zellerfeld), Dr. R. Müller (Clausthal-Zellerfeld), Dr. A. Nel (Paris; France), Prof. Dr. Ren D. (Beijing; China), Prof. Dr. A.P. Rasnitsyn (Moscow), Dr. C.-D. Sattler, Prof. Dr. J.W. Schneider, Dr. S. Schultka (Berlin; Germany), Dr. D. Shcherbakov, Dr. C.K. Shih (Beijing), Prof. Dr. A.W. Steffan (Biebergmünd; Germany), Prof. Dr. J. Rust, Dr. T. Wappler (Bonn), and especially Prof. Dr. J. Prokop (Prague; Czech Republic) for supportive remarks and cooperation.

For the discussion on bivalve ontogeny, anatomy, and ecology the author acknowledges (in alphabetical order): Prof. Dr. M.R.W. Amler (Munich; Germany), Dr. R. von Cosel (Paris), G. Falkner (Munich), Prof. Dr. G. Haszprunar (Munich), and Dr. S. Huwe (Hafrsfjord; Norway).

Dr. D. Korn (Berlin) is thanked for his support of the re-deformation of ammonoids.

Furthermore, the work would not be possible without the private collectors who provided their material. They are (in alphabetical order): H. Bech (Fröndenberg/Ruhr; Germany), the Hoffmann family (Hagen; Germany), Prof. Dr. M. Kemper (Amsterdam; The Netherlands),

L. Koch (Ennepetal; Germany), W. Sippel (Ennepetal; Germany), and G. Sommer (Schleusigen; Germany).

The two student assistants B. Kempf, and K. Schlüter administered to the work by managing numerous measurements and producing spreadsheets.

The author gained access to the material from the LWL-Museum für Naturkunde, Westfälisches Landesmuseum mit Planetarium (Münster). He sincerely thanks Dr. A. Hendricks and Dr. L. Schöllmann for their courtesy.

Not least, the author expresses his warmest thanks to his family for financial support, endurance, longanimity, and having the patience of a saint. H. is thanked for remembering him that there is even more in the world than Fossil insects.

The author gratefully acknowledges the financial support provided by the DFG (Deutsche Forschungsgemeinschaft) projects BR 1253/4-1 and BR 1253/4-2.

He also gained a financial travel support by the conference committee of "The 5th International Conference on Fossil Insects, Arthropods and Amber" hosted by the Nanjing Institute of Geology and Palaeontology (NIGP), Capital Normal University (CNU) and the Chinese Academy of Sciences (CAS) in Beijing (China). Exceptionally, the author acknowledges Prof. Dr. Ren D. for his advocacy.

Contents

Abstract

The fossil record of winged insects (Pterygota) begins slightly before the Mississippian–Pennsylvanian boundary (Early–Late Carboniferous) in the latest Mississippian. Usually there are only isolated wings or wing fragments known so that it is hardly possible to make conclusions about the paleo-ecosystems and the taphonomy of the Lagerstätten from this period.

Hagen-Vorhalle (Namurian B, late Marsdenian, zone R2c) stands out from all other Carboniferous Lagerstätten: More than 300 specimens of fossil insects have been found from Hagen-Vorhalle during the last three decades. Most of them are very well preserved and both positive and negative prints are known.

In this thesis the author presents conclusions on the development of the paleo-ecosystem of the Konservat-Lagerstätte and its complex multiechelon taphonomic processes arrived at by studying preservation patterns and the coexistence of different taxa.

A number of previously unrealized anatomical characters have been found during the revision of the complete material. For example, the first evidence for prothoracic winglets in basal Neoptera was found in one specimen of *Kochopteron hoffmannorum*.

In Hagen-Vorhalle a very special pattern of preservation is common in the material: Virtually all of the ~210 specimens of Neoptera lack an abdomen whereas it is always present in all palaeopterous specimens which also bear a number of appendages (e.g. genitalia). This work presents the first evidence for abdomens morphology in basal Neoptera. It can be found in three specimens of *K. hoffmannorum* and is associated with lacinial ovipositors. Furthermore details of the legs and a pentamerous tarsus are visible.

With *Baryshnyala occulta* (basal Neoptera: Baryshnyalidae) a new, so far overlooked very small Neoptera species is described. Due to its wing venation pattern it is discussed in this work as a possible exemplar of the most ancient Endopterygota.

Special focus was on the reconstruction of the taphonomy of Hagen-Vorhalle. In this context the coexistence of Neoptera and attached prodissoconchs of the bivalve *Naiadites vorhallensis* (Myalinidae) was used to show that Neoptera corpses underwent a period of pycnoclinal drifting in contrast to “Palaeoptera”. This presupposes a well-stratified water column as is plausible for a paleo-ecosystem related to a prograding birdfoot delta complex. A self-consistent model with six stages was conceptualized that takes in account all parameters.

Based on the findings from Hagen-Vorhalle a new Lagerstätte in the Ruhr area was explored. This led to the proof of some Pterygota from an outcrop at the Küchenberg near Fröndenberg/Ruhr. In addition to an already known isolated specimen of *Kemperala hagenensis* (Paolidae) exemplars of *Homaloneura berenice* (Spilapteridae) and *Bechala sommeri* (Bechalidae) were discovered. The locality shows strong parallels to Hagen-Vorhalle but is more terrestrially-dominated and most probably slightly younger (Namurian B/C, higher Ziegelschiefer Formation to Sprockhövel Formation).

Zusammenfassung

Der Fossilbericht der geflügelten Insekten (Pterygota) beginnt bereits kurz vor der Wende Unter-/Oberkarbon (Mississippian/Pennsylvanian) im obersten Unterkarbon. In der Regel liegen allerdings nur Einzelfunde oder Flügelbruchstücke vor, so dass Aussagen über das Paläo-Ökosystem nur begrenzt möglich sind. Gleiches gilt für die Rekonstruktion der taphonomischen Vorgänge, die zur Bildung von Fossillagerstätten geführt haben.

Unter den karbonischen Lagerstätten sticht Hagen-Vorhalle (Namurium B, oberes Marsdenium, Zone R2c) besonders hervor: Die vor dort in den letzten drei Jahrzehnten geborgenen Insektenfossilien sind mit über 300 Exemplaren sehr individuenreich vertreten und zudem außerordentlich gut erhalten. Meist liegen die Funde als Positiv- und Negativplatte vor und sind nahezu vollständig erhalten.

Die vorliegende Arbeit versucht, anhand des Erhaltungsmusters und des gekoppelten Vorkommens verschiedener Taxa Rückschlüsse auf die Entwicklung des Paläo-Ökosystems der Konservatlagerstätte zu ziehen sowie die komplexen, mehrstufigen Prozesse während der Taphonomie der Insekten zu rekonstruieren.

Eine Reihe von bisher nicht erkannten anatomischen Merkmalen konnten bei der Sichtung des gesamten Materials beschrieben werden. So gelang erstmals der Nachweis von Prothoracalflügelchen innerhalb der basalen Neoptera an einem Exemplar von *Kochopteron hoffmannorum*.

Ein spezielles Erhaltungsmuster der Neoptera von Hagen-Vorhalle ist das vollständige Fehlen eines Abdomens bei nahezu allen der ~210 Exemplare. Bei den palaeopteren Gruppen hingegen ist dieses grundsätzlich erhalten und zeigt zudem eine Reihe von Abdominalanhängen (z.B. auch Genitalapparate). Mit dieser Arbeit gelang es erstmals ein Abdomen bei den basalen Neoptera nachzuweisen. Es handelt sich bei den Stücken um drei weibliche Individuen von *K. hoffmannorum* mit ausgezeichnet erhaltenen lacinialen Ovipositoren. Weiterhin wurden auch Details aus dem Bau der Beine und eines fünfgliedrigen Tarsus sichtbar.

Mit *Baryshnyala occulta* (basale Neoptera: Baryshnyalidae) wurde eine neue, bisher übersehene Art sehr kleiner Neoptera beschrieben. Aufgrund des Flügeladerungs-Musters wird in dieser Arbeit diskutiert, ob es sich bei dem Einzelfund um den erdgeschichtlich ältesten Vertreter der Endopterygota handeln könnte.

Besonderes Augenmerk lag auf der Rekonstruktion der Taphonomie von Hagen-Vorhalle. Hier konnte durch das gekoppelte Vorkommen von Neoptera und anhaftende Prodissoconche der Muschelart *Naiadites vorhallensis* (Myalinidae) gezeigt werden, dass die Leichen der Neoptera, im Gegensatz zu denen der „Palaeoptera“ eine Phase der Pyknoklinaldrift durchlaufen. Hierzu ist eine gut geschichtete Wassersäule Voraussetzung, wie sie für das Paläo-Ökosystem in einem progradierenden Vogelfußdelta plausibel ist. Für den Vorgang konnte ein sechsstufiges Modell entworfen werden, das widerspruchsfrei alle Parameter berücksichtigt.

Ausgehend von den Erkenntnissen, die bei der Erforschung von Hagen-Vorhalle gewonnen werden konnten, wurde die Exploration von neuen, in etwa gleich alten Lagerstätten im Ruhrkarbon forciert. Dies führte zum Nachweis mehrerer Pterygota aus einem Aufschluss am Küchenberg bei Fröndenberg/Ruhr. Neben einem bereits bekannten Exemplar von *Kemperala hagenensis* (Paoliidae) sind dies Stücke von *Homaloneura berenice* (Spilapteridae) und *Bechala sommeri* (Bechalidae). Die Lokalität zeigt starke Parallelen zu Hagen-Vorhalle, ist aber stärker terrestrisch geprägt und wahrscheinlich etwas jünger (Namurium B/C; höhere Ziegelschiefer- bis Sprockhövel-Formation).

Part I

Introduction and general aspects

1 Introduction

Insects are the by far most diverse group of animals in Recent habitats and occur with presumably more than five million species (GASTON 1991; MORA et al. 2011). The actual number of species may even be much higher (up to 30 million species) and can hardly be captured.

Insects and some primary apterygote (wingless) groups are allocated to the taxon Hexapoda LATREILLE, 1825 (from Ancient Geek ἕξ [heks] = six and πούς [pous] = foot). The fossil record of this group begins in the Devonian (ca. 416–359 Ma). Oldest remains come from the Early Devonian of the Rhynie Chert in Aberdeenshire (Schottland, UK; HIRST & MAULIK 1926) and the Gaspésie (or Gaspé Peninsula) in Quebec (Canada; LABANDEIRA et al. 1988). Others come from the Middle Devonian of the Gilboa Fossil Forest in Schoharie County (New York State, USA; SHEAR et al. 1984). All of these findings are remains of apterygote Hexapoda.

The Lower Devonian species *Devonohexapodus bocksbergensis* HAAS et al., 2002 (see also HAAS 2005) from the Hunsrück Slate (early Emsian; Germany) has been described as an ancient representative of Hexapoda. This interpretation has been disproved by WILLMANN (2005) and KÜHL & RUST (2009).

Rhynie speciems are mostly Collembola LUBBOCK, 1873 (springtails). They can be allocated together with Diplura BÖRNER, 1904 and Protura SILVESTRI, 1907 (coneheads) to the Entognatha HIRST & MAULIK, 1926, the adelphotaxon of Insecta LINNAEUS, 1758 (from Latin insectum = cut into sections) within the Hexapoda. Furthermore *Rhyniognatha hirsti* TILLYARD, 1928 is only known from its chewing-biting mouthparts. Due to the modern appearance of the mandibles ENGEL & GRIMALDI (2004) and GRIMALDI & ENGEL (2005) interpreted it to be an early Pterygota BRAUER, 1885 (i.e. winged insects; from Ancient Geek πτερόν [pterón] = wing). PROKOP et al. (2005) disputed this and a nonambiguous proof of the coherency between the characteristics of the mandibles and the presence of wings has yet to be given.

From the two locations in North America there come just a few, very tiny and broken remains which were interpreted as Insecta close related to Archaeognatha BÖRNER, 1904 (jumping bristletails). However, this attribution is controversial due to the poor preservation.

The oldest definitive Pterygota remain is a broken part of a (probably) Neoptera wing recently described by PROKOP et al. (2005) from the Lower Namurian of the Czech Republic (Petřkovice Beds; Pendleian, Namurian A, lower E1; see Fig. 1). The specimen was found inside a drilling core sample. Due to its poor preservation neither a species nor a genus nor even a family was given to it. It has been published as an unnamed “Archaeorthoptera inc. sed”.

In 1996 the oldest complete preserved Pterygota was discovered and described as *Delitzschala bitterfeldensis* BRAUCKMANN & SCHNEIDER, 1996 (Palaeodictyoptera GOLDENBERG, 1877: Spilapteridae HANDLIRSCH, 1906). It was also found within a core sample from a deep drilling in the coal mining area of Bitterfeld/Delitzsch of Saxony-Anhalt and Saxony (eastern Germany) from the Latest Mississippian (Namurian A, Arnsbergian).

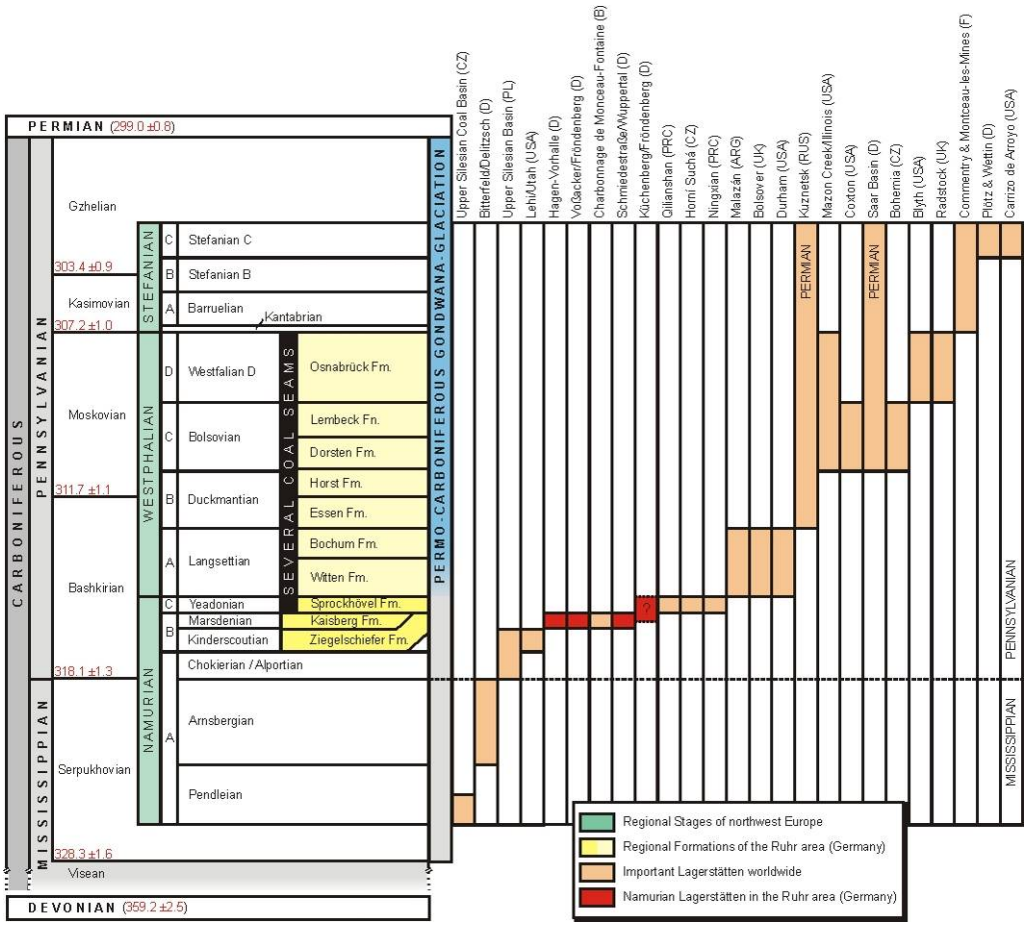


Fig. 1: Stratigraphic overview of important Carboniferous winged insect Lagerstätten worldwide. The fossil record of the Pterygota BRAUER, 1885 begins in the latest Mississippian. Important Namurian Lagerstätten of the Ruhr area in western Germany are highlighted in red.

So, the well-founded fossil record of Pterygota begins in the Namurian. The rocks of the Konservat-Lagerstätte Hagen-Vorhalle (late Marsdenian; western Germany) also date in this period but are slightly younger than those from Bitterfeld/Delitzsch. All other Pterygota remains from other localities worldwide seem to be (at least slightly) younger than the specimens from Hagen-Vorhalle.

In the last few years new taxa have been described from the Czech Republic and Poland (e.g. PROKOP et al. 2010, in press. and further references therein) and China (e.g. PENG et al. 2004; PROKOP & REN 2007).

Pterygota become much more common during the Westphalian (late Bashkirian to Moskovian) and Stephanian (Kasimovian to early Gzhelian). The Mazon Creek fossil beds near Morris in Grundy County (Illinois, USA; Westphalian D) comprise a prominent Lagerstätte. Roughly contemporaneous, but by far not as well preserved, are the specimens from the Piesberg near Osnabrück (western Germany; see BRAUCKMANN et al. 2009 and further references therein).

Another very important locality is Commentry in the department of Allier (central France) that bears rocks and fossil insects of the Stephanian B (close to the Kasimovian/Gzhekian

boundary). It is famous for its giant odonates. Montceau-les-Mines is approximately of the same age and lies 130 km NE of Commentry in the department of Saône-et-Loire.

In Germany Early Permian Pterygota are well known from the Saar–Nahe Basin in the south west which is probably one of the most important localities of this period worldwide. It has delivered more than 90 species and at least 59 specimens in open nomenclature (BRAUCKMANN et al. 2010).

During the last 29 years, a unique flora and fauna has been recovered in the former brickyard quarry of Hagen-Vorhalle. And among the approximately 16,000 specimens there are about 310 insects. A large proportion of the material is quite completely preserved, including the oldest known completely preserved pterygote insects ever discovered.

In summary there is just a small number of localities that provided material older than the specimens from Hagen-Vorhalle. The latter are by far the best preserved fossil Pterygota for this period and were furthermore found in a high number of individuals of several taxa. This highlights the importance of the Konservat-Lagerstätte in western Germany for the reconstruction of Late Carboniferous ecosystems and the evolution of basal Pterygota worldwide.

This work gives an interpretation of the paleo-environmental history and reconstructs the taphonomy of the Lagerstätte. Furthermore a new insect Lagerstätte in approximately contemporaneous (probably slightly younger) rocks that was identified near Fröndenberg/Ruhr is discussed.

2 Locality – The Konservat-Lagerstätte Hagen-Vorhalle

2.1 Overview and mining history

Hagen-Vorhalle is located at approx. N 51° 22.88', E 007° 26.77' (UTM: grid zone 32U; geodetic datum: WGS84). Older German maps are mostly referenced to the Gauß–Krüger coordinate system (geodetic datum: Bessel 1841 reference ellipsoid). In this system the Lagerstätte is located at R ^{26}00660, H ^{56}95190. The elevation is ~115 m a.s.l. (i.e. Normalnull).

Following important maps label the Lagerstätte:

- Topographic map of North Rhine-Westphalia 1:25,000, sheet no. 4610 Hagen/Westfalen;
- Geologic map of North Rhine-Westphalia 1:25,000, sheet no. 4610 Hagen/Westfalen;
- Geologic map of North Rhine-Westphalia 1:100,000, sheet no. C4710 Dortmund;
- Geologic general map of North Rhine-Westphalia 1:500,000.

Hagen is a city in western Germany with a population of almost 200,000 people. It is located in the center of the federal state North Rhine-Westphalia (Nordrhein-Westfalen), south of the river Ruhr and west of the river Volme (Fig. 2). The surrounding urban agglomeration is called the Ruhr Metropolitan Region (Ruhrgebiet) which was once one of the most important and productive mining and heavy industry districts of Europe an which now has a population of today about 5.2 million people.

Northwest of Hagen, within the urban district Vorhalle, a rich fossil ecosystem was found in the opencast pit of a former brickyard quarry. It is located southeast of the road Sporbecker Weg, close of the today's federal motorway BAB 46.

Mining activity by the brick production company Vorhaller Klinkerwerke took place north of the road from 1853–1967. The bricks were mainly used in tunneling, chimney construction and canalization as they were acid-resistant and high-pressure proof. In 1968 a new quarry was opened south of the road Sporbecker Weg. The first fossils, mainly plant remains, were found during this later mining period.

In 1986 the company brought brick production to an end after 133 years of fabrication in the area around Hagen. This enabled the Westfälisches Museum für Naturkunde in Münster to arrange excavation campaigns (see follwing chapter 2.2).

As early as the 1970s there were ambitions to preserve the pit due to its unique tectonics and plant fossils. But not until an extraordinary Arthropoda LATREILLE, 1829 fauna was discovered in 1982 was the site provisionally designated as a listed monument. Prior to this, not unlike the UNESCO World Heritage Site Grube Messel near Darmstadt, it was planned to use the open pit

as a local garbage dump. This danger was averted in 1993 with the definitive incorporation of the quarry in the list of monuments of the city of Hagen. Today it is managed as ground monument (Bodendenkmal) no. 4610, 15.

Nowadays the pit is still well preserved in form and shape. Some pioneer plants have spread out meanwhile—like Poaceae (true grasses), Betulaceae (birches) and Coryloideae (hazels).

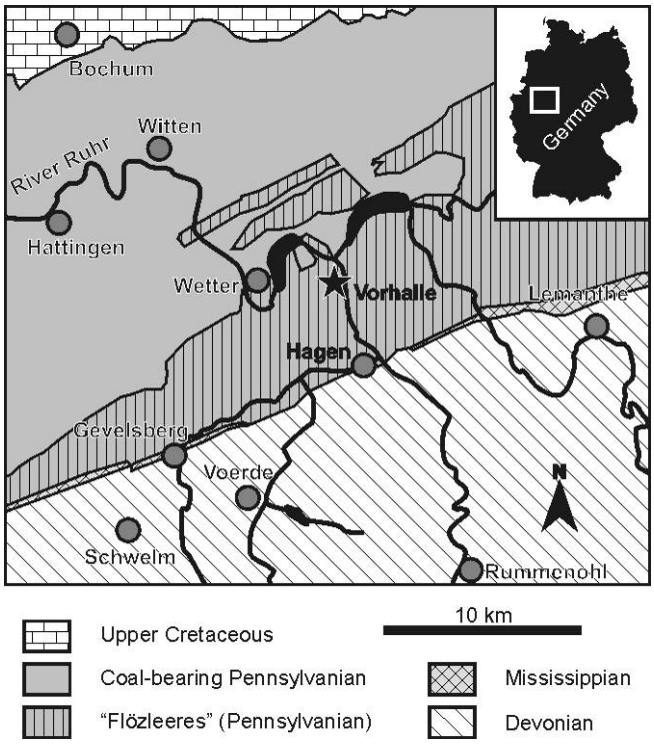


Fig. 2: Geological Overview map of Hagen-Vorhalle. Carboniferous strata are drawn in gray. Modified after SCHÖLLMANN (2005).

2.2 Paleontological exploration history

Recently SCHÖLLMANN (2005) gave an overview of the exploration history. The first scientific report of fossil material from the brickyard quarry of Hagen-Vorhalle is given by FRANKE (1928). Mining and digging activity had delivered a divers paleo-flora which has been described in the following years by e.g. GOTHAN (1929; 1931; 1935; 1941; 1953), GOTHAN et al. (1959), and REMY & REMY (1977). It is also mentioned in the work by JOSTEN (1983; 1991). The occurrence of distinct taxa gave first insights to the stratigraphical position of the Vorhalle strata.

Bivalvia LINNAEUS, 1758 and ammonoids were the first faunal elements which had been described form the Lagerstätte (HAHNE 1930). Especially the latter were intensively described by PATTEISKY (1959; 1965). He improved the biostratigraphical interpretation of Hagen-Vorhalle by the use of ammonoid index fossils (see chapter 2.4.1).

The first Arthopoda was found by the private collector L. Koch in 1982. It was a specimen of *Prothelyphonus naufragus* BRAUCKMANN & KOCH, 1983 (Arachnida CUVIER, 1812: Thelyphonida

LATREILLE, 1804 = Uropygi; colloquial vinegaroons or whip scorpions). In the following years the number of arthropods increased significantly by the work of the Hoffmann family, M. Kemper, L. Koch, and W. Sippel in cooperation with C. Brauckmann from the Fuhlrott-Museum (Wuppertal; Germany) and lead to many scientific publications (a complete list until this date is given by BRAUCKMANN et al. 2003: 62–65) and popular science books (e.g. Koch 1984; 1988). An overview of the paleo-fauna was presented by BRAUCKMANN et al. (1985).

When mining activity came to an end in 1982 the Paläontologische Bodendenkmalpflege für Westfalen-Lippe and the Westfälisches Museum für Naturkunde (today re-named to LWL-Museum für Naturkunde, Westfälisches Landesmuseum mit Planetarium) in Münster (Germany) were able to organize an intensive excavation campaign from 1990 to 1997. Important recoveries were made during this period and increased the number of specimens (both floral and faunal) to 16,000, mostly with positive and negative print. Again, most common fossils were plants, ~310 of the specimens were Pterygota BRAUER, 1885. BRAUCKMANN et al. (2003) gave a circumstantial overview of all up to this date known taxa of Arthropoda from Hagen-Vorhalle, including many new descriptions of taxa.

Most recently a number of publications by BRAUCKMANNN et al. (2005; 2007; 2010) and ILGER & BRAUCKMANN (2007; 2008; 2009) reported new evidences and findings from the material of the private collectors and the official excavation campaign.

2.3 Supra-regional importance (with a list of taxa)

Hagen-Vorhalle is a locus typicus for many faunal and floral taxa. Along with numerous plant fossils it became famous for its highly diverse basal Pterygota and rare Arachnida with surprisingly well preserved specimens. The international importance of Hagen-Vorhalle for the knowledge of Late Carboniferous fauna and flora lies in the extraordinarily well-preserved fossils and in their high age.

During the excavation campaign from 1990–1997 the Westfälisches Museum für Naturkunde was able to recover 16,000 fossils overall. They have been allocated to sub-clades of "algae" s.l., Articulatae , Lycopsida, Pteridophylla, and Coniferopsida. A list of all taxa is given by HENDRICKS (2004: 218–219). The paleo-flora has been described in detail by JOSTEN & VAN AMEROM (1999) where further references can also be found.

Moreover significant faunal elements were also found. They can be attributed to the following taxa (see HENDRICKS 2004: 216–217 for detailed list of all taxa):

Mollusca CUVIER, 1797
- Bivalvia LINNAEUS, 1758
- Gastropoda CUVIER, 1797
- Cephalopoda CUVIER, 1797

Arthropoda LATREILLE, 1829
Arachnida LAMARCK, 1801
Crustacea BRÜNNICH, 1772
"Myriapoda"-like Arthropods
Hexapoda LATREILLE, 1825
Eurypterida BURMEISTER, 1843
Brachiopoda DUMÉRIL, 1806
Crinoidea MILLER, 1821
Conodonta PANDER, 1856
Vertebrata CUVIER, 1812
"fish" s.l.
Amphibia GRAY, 1825

Summarized with the umbrella term "fish" there were found Acanthodii OWEN, 1846 (also known as "spine sharks," see HEIDTKE (1995)), Xenacanthiformes FRITSCH, 1889, Actinopterygii COPE, 1871, Coelacanthiformes BERG, 1937, and Rhipidistia COPE, 1887.

The entire bivalve fauna of Hagen-Vorhalle has been outlined by HUWE & AMLER (2003; 2005) and been described in detail by HUWE (2006) who considered ~770 specimens, mostly with positive and negative prints. The fauna accounts for ~90% of *Naiadites vorhallensis* HUWE, 2006 which is well known from all ontogenetic stages. About ~7% of the bivalves belong to the genus *Anthraconaia* TRUEMAN & WEIR, 1946 which is divided into four species: *A. beatae* HUWE, 2006, *A. hagenensis* HUWE, 2006, *A. melari* HUWE, 2006, and *A. schoellmanni* HUWE, 2006. The remaining ~3% are composed of *Posidonia* cf. *corugata* (ETHERIDGE JR., 1874), "*Modiolus*" *patulus* (M'COY, 1844), and "*Modilus*" sp. A.

Due to their size and shape all prodissoconchs and dissoconchs reported in this paper can be allocated to the species *Naiadites vorhallensis* HUWE, 2006.

Fossil insects are of strong importance for the reconstruction of paleo-ecosystems and taphonomy. Usually they are highly diverse in Fossil and Recent ecosystems and also occur in high numbers of individuals. From Hagen-Vorhalle at least twenty species of Pterygota are known. Together with the exceptionally well-preserved findings of ancient Arachnida (see e.g. BRAUCKMANN et al. (1985; 2003)) they insure the super-regional importance of the Lagerstätte for the understanding of paleo-ecosystems in the Late Carboniferous and the taphonomic processes that led to this kind of type of deposit.

"Palaeoptera" (see chapter 4 for remarks on this probably non-monophyletic group) have proven to be highly diverse in Hagen-Vorhalle. They can be allocated to five orders with at least fourteen species. On the other hand Neoptera are represented by only five species in one order.

From another point of view this proportion reverses: Neoptera comprise ~68% ($n \approx 210$) of

all specimens whereas "Palaeoptera" make up the remaining ~32% (n ≈ 100).

In summary the paleo-ecosystem was strongly dominated by a few taxa of Neoptera with a subordinated, but diverse, attending "Palaeoptera" fauna. These proportions are consistent with other approximately contemporaneous Lagerstätten. A good example is the entomofauna of the Upper Silesian Coal Basin which has recently been described by PROKOP et al. (2010; in press, comprising the Porąbka-Klimontów coal mine in Sosnowiec in Poland and Horní Suchá in the Czech Republic).

Nearly all described insect species are endemic to Hagen-Vorhalle—except for *Kemperala hagenensis* BRAUCKMANN, 1984 and *Homaloneura berenice* BRAUCKMANN & GRÖNING, 1998, which are also known from the probably slightly younger strata of the Küchenberg locality near Fröndenberg (see chapters 3.3.2, 7, and SCHULTKA (1995)). Furthermore many of the insect taxa from Hagen-Vorhalle represent the stratigraphically oldest known evidence of their family. One of the few exceptions is *Delitzschala bitterfeldensis* BRAUCKMANN & SCHNEIDER, 1996 (Palaeodictyoptera GOLDENBERG, 1877: Spilapteridae HANDLIRSCH, 1906) from the late Early Carboniferous (Namurian A; Arnsbergian) of the area around Bitterfeld–Deltizsch (Saxony-Anhalt, Germany; approx. N 51° 35', E 012° 20'). The probably oldest known representative of the Pterygota in general is a Neoptera wing fragment described as "Archaeorthoptera indet." by PROKOP et al. (2005) from the latest Early Carboniferous (Namurian A; Pet kovice Beds; Pendleian; lower E1) of the Upper Silesian Basin in the Czech Republic. All other findings of Insecta LINNAEUS, 1758 from the Namurian seem to be stratigraphically younger than Hagen-Vorhalle. Usually these are preserved as isolated wings or fragments of wings.

Eight of the nineteen species of Pterygota can be allocated to the Palaeodictyoptera GOLDENBERG, 1877. In German they were formerly called "Urnetzflügler," a term which can often be found in older literature. They are:

Family Homoiopteridae HANDLIRSCH, 1906
Homoioptera BRONGNIART, 1893
Homoioptera vorhallensis BRAUCKMANN & KOCH, 1982

Family Spilapteridae HANDLIRSCH, 1906
Homaloneura BRONGNIART, 1885
Homaloneura ligeia BRAUCKMANN, 1986
Homaloneura berenice BRAUCKMANN & GRÖNING, 1998

Family Lithomantidae HANDLIRSCH, 1906
Lithomantis H. WOODWARD, 1876
Lithomantis varius BRAUCKMANN in BRAUCKMANN et al., 1985

Family Graphiptilidae HANDLIRSCH, 1906
Patteiskya LAURENTIAUX, 1958
Patteiskya volmensis (BRAUCKMANN, 1984)

Family Breyeriidae HANDLIRSCH, 1906
Jugobreyeria BRAUCKMANN in BRAUCKMANN et al., 1985
Jugobreyeria sippelorum BRAUCKMANN in BRAUCKMANN et al., 1985

Family Dictyoneuridae HANDLIRSCH, 1906
Dictyoneura GOLDENBERG, 1854
Dictyoneura kemperi BRAUCKMANN & KOCH, 1983

Family Archaemegaptilidae HANDLISCH, 1919
Archaemegaptilus MEUNIER, 1908
Archaemegaptilus schloesseri BRAUCKMANN et al., 2003

Megasecoptera BRONGNIART, 1885 are closely related to this taxon and occur with only two small representatives:

Family Bardohymenidae G. ZALESSKY, 1937
Sylvohymen MARTINOV, 1940
Sylvohymen peckae BRAUCKMANN, 1988
Sylvohymen pintoi BRAUCKMANN et al., 2003

Likewise closely related to the Megasecoptera—and formerly fused with them into one single taxon—are the Diaphanopterodea HANDLIRSCH, 1919 (= Paramegasecoptera). In Hagen-Vorhalle is only one species:

Familie Namurodiaphidae KUKALOVÁ-PECK & BRAUCKMANN, 1990
Namurodiapha KUKALOVÁ-PECK & BRAUCKMANN, 1990
Namurodiapha sippelorum KUKALOVÁ-PECK & BRAUCKMANN, 1990

The Odonatoptera Martynov, 1932 (= Libellulidae sensu RASNITSYN & PRITYKINA, 2002; in German formerly called “Urlibellen”) occur with four species:

Neodonatoptera BECHLY, 1996
Eomeganisoptera“ ROHDENDORF, 1962
Family „Erasipteridae“ CARPENTER, 1939
Erasipteroides BRAUCKMANN & ZESSIN, 1989

Erasipteroides valentini (BRAUCKMANN in BRAUCKMANN et al., 1985)
Zessinella BRAUCKMANN, 1988
Zessinella siope BRAUCKMANN, 1988
Rasnitsynala ZESSIN et al., in press
Rasnitsynala sigambrorum ZESSIN et al., in press

Meganisoptera MARTYNOV, 1932
Family Namurotypidae BECHLY, 1996
Namurotypus BRAUCKMANN & ZESSIN, 1989
Namurotypus sippeli BRAUCKMANN & ZESSIN, 1989

Neoptera have been described in five species from Hagen-Vorhalle (please attend to the systematic remarks below):

Family Paoliidae HANDLIRSCH, 1906
Kemperala BRAUCKMANN, 1984
Kemperala hagenensis BRAUCKMANN, 1984
Holasicia KUKALOVÁ, 1958
Holasicia rasnitsyni BRAUCKMANN, 1984

Family ?Cacurgidae HANDLIRSCH, 1911
Kochopteron BRAUCKMANN, 1984
Kochopteron hoffmanorum BRAUCKMANN, 1984
Heterologopsis BRAUCKMANN & KOCH, 1982
Heterologopsis ruhrensis BRAUCKMANN & KOCH, 1982

Family Baryshnyalidae
Baryshnyala
Baryshnyala occulta

Systematic remarks: *K. hagenensis* and *H. rasnitsyni* can be assigned to the family Paoliidae HANDLIRSCH 1906. For diagnosis and included genera see KUKALOVÁ (1958), BRAUCKMANN (1984), BRAUCKMANN et al. (1985; 2003; 2010), PROKOP & NEL (2007), ILGER & BRAUCKMANN (2008) and PROKOP et al. (in press). As shown in the historical compilation by PROKOP & NEL (2007), the systematic rank of "paoliids" and related early Pterygota has been the subject of controversy during the last few decades: CARPENTER (1992), for example, traditionally considered them as a family within the "Protorthoptera," a clearly polyphyletic "order". KUKALOVÁ-PECK & BRAUCKMANN (1992) assigned the "paoliid line" together with other early Neoptera to the "hemipteroid stem assemblage". GRIMALDI & ENGEL (2005) placed them as Paoliidae directly in Neoptera with-

out indication of any order. On the other hand, ROHDENDORF & RASNITSYN (1980) and subsequently RASNITSYN & QUICKE (2002) ranked them as Paoliida on ordinal level. PROKOP & NEL (2007) did the same, and additionally introduced their Katerinkidae PROKOP & NEL, 2007, a closely related new family of the same order. A more general critical discussion of different views of hexapod phylogeny including the "Palaeoptera"–Neoptera problem (see chapter 4) has been provided by KLASS (2007; 2009). In the present contribution a precise higher systematic assignment is avoided, because the author does not want to anticipate the final results of the current phylogenetic analyses. Therefore a broad comparison of significant characters in basal Neoptera from different Lagerstätten in Germany, Poland and the Czech Republic is in preparation.

The systematic position of *K. hoffmannorum* and *H. ruhrensis*—which are morphologically very similar to the Paoliidae—is unclear and still controversial. BRAUCKMANN et al. (2003) tentatively assigned them to the family ?Cacurgidae HANDLIRSCH, 1911. In contrast, BÉTHOUX & NEL (2002) placed *H. ruhrensis* in the Archaeorthoptera BÉTHOUX & NEL, 2002.

B. occulta cannot be allocated to any of these groups and represents a new family within the early Neoptera (Baryshnyalidae; see chapter 7.3 for systematic paleontology).

2.4 Stratigraphy and lithology

2.4.1 Stratigraphy

The rocks of this Konservat-Lagerstätte belong to the Ziegelschiefer Formation (German Ziegelschiefer = brick slate) of the Namurian B (late Marsdenian; early Late Carboniferous; Pennsylvanian: early Bashkirian). An absolute age is specified by different authors between approximately 310 to 319 million years (SCHÖLLMANN 2000; 2005; BECHLY et al. 2001).

Bio-stratigraphical dating has been done by the dint of a distinct index fossil. As the rock lack significant micro fossils it is based on the occurrence of the ammonoid species *Bilinguites metabilinguis* (WRIGHT, 1927) (Fig. 3), which was originally named *Reticuloceras superbilingue metabilingue*. It is strictly restricted to the zone R2c in ammonoid bio-stratigraphy. This species is the only index fossil found in the entire sequence. Floral elements from Hagen-Vorhalle support the ammonoid-based dating, but are not sufficient on their own as they may occur in under- and overlying strata as well.

Litho-stratigraphically the rocks of the Ziegelschiefer Formation belong to the so called "Flözleeres" (= without coal seams) which is followed by the coal bearing strata of the Namurian C (Yeadonian) to the latest Westphalian D.

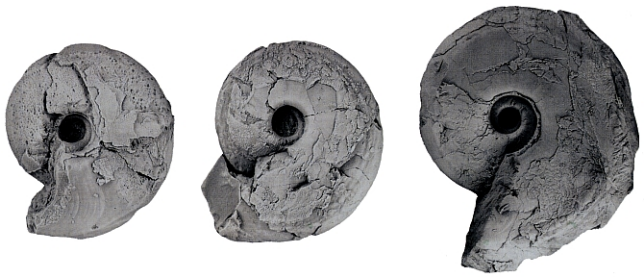


Fig. 3: Three very well preserved specimens of *Bilinguites metabilinguis* (WRIGHT, 1927), the only index fossil that can be found in the Ziegelschiefer Formation of Hagen-Vorhalle. Modified after KORN (2005).

2.4.2 Lithology

The rocks of the Ziegelschiefer Formation are mostly dark gray or virtually black shales and siltstones that vary in color from brownish to light gray (RICHTER 2005). The overall thickness of the entire formation is assessed to be about 400–600 m (e.g. RICHTER 1996). While the lower beds are mud-dominated, an increase in sandy layers towards the top mark a coarsening-upward trend. Distinct sandstone beds were interpreted by KRAFT (1992) as tempestites. Shales mainly consist of quartz, illite, and chlorite with varying amounts of mica (the latter three are phyllosilicates minerals). The rocks are clearly stratified with laminae ranging from 0.5–3 mm at an average of 0.8 mm (SCHÖLLMANN, 1999).

Fossil-bearing strata are restricted to laminated shales at the top of the sequence. Some layers are rich in fragmental plant remains which can build up thin, coaly strata. Others bear siderite concretions ($FeCO_3$), pyrite (FeS_2) or secondary calcium sulfate ($CaSO_4 \cdot 2H_2O$, i.e. gypsum).

KRAFT (1992) has described interstratified banks of sandstones with clay-fine matrix, small rock fragments and feldspars ("graywacke" rock type but of different genesis).

While weathering the sandstones become ocher–red in color (due to the high Fe-content) and finally crumble "sand-like" away. Whereas the slates keep their dark color and disrupt in chips.

2.5 Tectonics

At a regional scale the rocks belong to the northern flank of the Remscheid Anticlinorium. The tectonic pattern was described and interpreted in detail by DROZDZEWSKI et al. (1996) where further references can be found. Due to tectonic deformation and fragmentation a horizon-referenced recovery of the fossils is impossible—even during systematic and diligent excavation campaigns. However DROZDZEWSKI (1982) was able to use three distinct ammonoid-bearing horizons for the detailed stratigraphy.

At the pit's east wall a vivid folding pattern is visible and exhibits three anticlines (Fig. 4) with amplitudes and spreads between 20–40 m. Axial planes dip with an angle of 70–80° to the northwest. Tiny antithetic thrust faults in the dimension of centimeters or decimeters are abundant and almost normal to stratification. Synthetic faults occur where thrust faults and axial planes intersect. Additionally contrariwise dipping faults occur in steep anticline limbs and produce a fishtail-like disruption pattern.

All together the sequence is strongly folded and disrupted. Especially the tectonic elongation and compression must be considered when measurements and width/length ratios should be compared with each other. Measurements of strongly deformed ammonoids (mostly *Bilinguites metabilinguis* in different ontogenetic stages) have shown that the mean deformation factor (μD) in the direction of maximum elongation is μD = 1.21 ±0.093 (n = 41) (see chapter 3.2).

Fig. 4: Prominent anticlines in the former bickyard quarry of Hagen-Vorhalle. This photograph gives an impression of the strong tectonic deformation of the sediments. The official excavation campaign can be seen to the right. Modified after HENDRICKS (2005).

2.6 Paleo-geography and paleo-oceanography

The Late Carboniferous was a period of widespread basin sedimentation in Europe. The collision of Laurussia ("Old Red") in the north and Gondwana in the south generated the (sub-) equatorial Variscan orogen. Especially to the north of this mountain range a parallel basin was established by syn-orogenic subsidence in the foreland. During the Mississippian a flysch-type sedimentation took place that merged into a molasse type in the Pennsylvanian. The basin evolved to an epi-continental seaway with a complex bathymetric relief. Sandstones, shales and conglomerates from the Variscides were deposited in the sub-mountainous foreland and shallow basin. In western Germany the whole Pennsylvanian sequence can reach thicknesses >5,000 m (KOCH, 1988) but values may vary regionally.

Hagen-Vorhalle is located at the southern coast of the seaway where a river that drained the Variscides built up a prograding delta complex.

Globally, the Late Carboniferous was a cold period in earth history and the expanding Gondwana ice shield became established which led to the subsequent Permo–Carboniferous glaciation. As Hagen-Vorhalle lies close to the equator (Fig. 5) the thermal degradation was not as intense as at higher latitudes. This is supported by the fossil record, first of all by the floral elements (JOSTEN & VAN AMERON, 2003), that resemble a thermophile ecosystem.

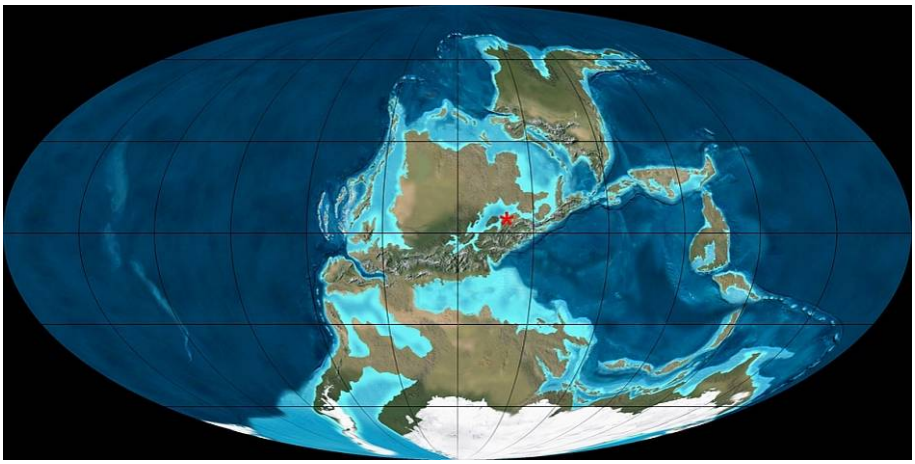


Fig. 5: Global paleo-geographic reconstruction of the Earth in the Late Carboniferous (Pennsylvanian) period ~300 million years ago. Approximate location of Hagen-Vorhalle is indicated by a red asterisk. Modified after BLAKEY (http://jan.ucc.nau.edu/~rcb7/)

Even if reduced to Recent levels there must be a remarkable grade of evaporation in the tropical seas. The loss of water to the atmosphere caused increasing seawater salinity. The process benefited from the landlocked setting of the seaway with only one narrow mouth to the Paleo-Tethys Ocean in the east. In a strict sense this ocean makes up itself a very large enclosed sea like the Recent Caribbean Sea. It was surrounded by the evolving Pangea in the north, west and south and separated from the Panthalassic Ocean by an island arc to the east. This may have amplified the effect of salinity enhancement in the seaway, too.

River systems drained the Variscides and transported freshwater and sediments to the submontane foreland and into the shallow marine basin. Their water was relatively warm and highly charged with sediments.

The tidal ranges (i.e. double tidal amplitude = vertical difference between high and low tide) in the seaway were reconstructed by WELLS et al. (2005a, 2005b) who created finite element methods to model the paleo-tidality. Their work was referenced by modeling tides in the Recent Mediterranean Sea which is of comparable architecture even though much smaller. The authors reasoned from their scenarios that there were no strong tidal ranges within the semi-enclosed Late Carboniferous seaway. This is due to intra-seaway islands like the Wales–Brabant Massif and others. Especially for the area of Hagen-Vorhalle they predicted very low tidal ranges both for a maximum sea-level scenario and a scenario with a hypothetical sea-level rise following a sea-level lowstand. Tidal ranges may have varied from 1–10 cm (WELLS et al. 2005a: 728, fig. 7E–

F). Reconstruction of eustatic sea-level changes in the Paleozoic has recently been carried out by HAQ & SCHUTTER (2008).

At these low grades of tidal mixing, in combination with the tropical heat and salinity enhancement, stratification in the open water body seems most likely (WELLS et al. 2005a). In a stratified water column the production of organic material would cause anoxia in the lower strata. This oxygen-free environment can explain the extraordinary preservation of the Konservat-Lagerstätte Hagen-Vorhalle. The assumption of an anoxia is supported by the occurrence of pyrite (FeS_2; see chapter 2.4.2) and an enrichment of organic carbon (C_{org}) generating the dark color of the rocks.

Sediments bear an assemblage of marine, brackish and non-marine organisms, partly associated with each other. Furthermore C/O isotope analysis was made in early-diagenetic Ca-siderite concretions and referenced to data by MOZLEY & WERSIN (1992). According to these values of $\delta^{13}C$ and $\delta^{18}O$ best fit to an interfingering facies of marine and terrestrial deposits (RICHTER 2005).

The most plausible setting is a birdfoot delta with many active and inactive channels and intercalated lagoons and bayous. Due to the high rate of sediment input and predominant lack of counter-action like tides, waves and marine currents the delta prograded in several distributaries into the basin (e.g. EINSELE, 2000). The irregular alternating of active and inactive channels led to jigsaw-type interfingering of marine and non-marine lithology and paleontology. HUWE (2006) came to the same results through her syn-ecological reconstruction on the basis of bivalves and other taxa.

This model is supported by the sedimentological work of BRETTLE et al. (2002) who reconstructed a fluvial-dominated delta system of the contemporaneous Pennine Basin that is a part of the epi-continental seaway between the Askrigg Block and the Wales–Brabant Massif.

A Recent analog is the Mississippi delta (RICHTER 2005). Its birdfoot-like shape is steady (but not static) as the Gulf of Mexico set in an embayed basin also with very low tidal ranges. That a strongly stratified water body is stable and can be very long-lasting in time and space under open sea conditions has recently been shown by HU et al. (2005). These authors showed by means of NASA satellite images a freshwater plume deriving from the Mississippi river mouth into the Gulf of Mexico. This plume can be tracked all the way around the Florida peninsula up to Georgia and South Carolina.

Nevertheless single events like hurricanes and heavy thunderstorms can temporarily perturb these conditions and high-energetic accumulations like the tempestites described by KRAFT (1992) will be deposited. Subsequently the system returns to its regular deltaic sedimentation and water stratification.

2.7 Konservat-Lagerstätte – A special type of deposit

The term Lagerstätte (plural: Lagerstätten) is a loanword from German for a fossil bearing sedimentary deposit (literally "storage place") which has been introduced by SEILACHER (1970). In German it is also used for other kinds of geological deposits like ore deposits, minerals resources, and gas/oil deposits. In English it is strictly reserved for paleontological aspects.

In general fossils from a Lagerstätte can either be autochthonous (from Ancient Greek αύτός [autós] = self or same and χθών [chtón] = earth) or allochthonous (άλλος [állos] = other). In the first case fossils have once lived and died at the same place where they are embedded in the sediment. There was no taphonomic transport of the corpses. In the case of allochthony the fossils have been secondarily transported to the place of their final embedding. Usually this has caused damage to the body.

In most cases there is not one single species in the fossil record of a Lagerstätte but a number of co-embedded groups of organisms. They can either build up a thanatocenosis (from Ancient Greek θάνατος [thánatos] = death and κοινός [koinós] = together) or a taphocenosis (τάφος [táphos] = burial). A thanatocenosis (sensu WASMUND 1926) is a community of dead bodies that can either be autochthonous or allochthonous. A taphocenosis (sensu QUENSTEDT 1927) is a thanatocenosis that is build up of autochthonous and allochthounous (also originally autochthounous but secondarily transported) fossil elements that are embedded in the sediment. Hagen-Vorhalle is an allochthonous taphocenosis.

Furthermore there are two different kinds of Lagerstätten: the Konzentrat-Lagerstätte (also concentration Lagerstätte), and the Konservat-Lagerstätte (also conservation Lagerstätte). A typical example of Konzentrat-Lagerstätten are bone beds, i.e. distinct strata within a sedimentary sequence that bear a high number of fossil bones (e.g. the Dinosaur National Monument on the boundary of Colorado and Utah). Konservat-Lagerstätten on the other hand are known for their extraordinarily well preserved specimens exhibiting even soft parts of the body. Hagen-Vorhalle is a prominent example for this type as Arthropoda and other groups show many characters rich in details.

For the formation of a Konservat-Lagerstätte some preconditions have to be realized: (i) embedding has to take place very fast, before biological decomposition can progress, (ii) the environment has to be oxygen-free to suppress oxic bacterial recycling, and (iii) the sediment has to be fine-grained (e.g. siltstone or mudstone) as too coarse grains (as in sandstones) would not be able to reproduce tiny structures. Furthermore the period between death of the organism and its embedding—i.e. the time of drifting or other transport of the corpse—has to be either very short or at least without any disturbance by predators, scavengers or mechanical disruption etc.

Hagen-Vorhalle is an extraordinary example for this kind of Konservat-Lagerstätte. Fossils are preserved as thin graphitic layers of thicknesses less than 10 µm (QUETSCHER & ILGER 2007). Additionally to the marvelous richness in details there are mostly both positive and negative plates known of the specimens. Due to diagenetic and tectonic compression the three-

dimensional structure is smoothed out but not completely plane. Again, this is of significant importance for the interpretation of characters in Pterygota. Insect wings usually show a virtual corrugation which is correlated to distinct major longitudinal ("main") veins (see chapter 3.4).

Winged insects occur in two major groups: "Palaeoptera and Neoptera (see chapter 2.3). The fossil record of Hagen-Vorhalle reveals significant differences in the preservation pattern between the two groups of Pterygota (Fig. 6): "Palaeoptera" are mostly completely preserved and show fragile structures like filiform antennae, tiny tarsomeres with spines and hairs, abdominal appendages with extremely long cerci and genital apparatuses. By contrast, Neoptera show many comparable features (antennae, legs) but almost always lack the abdomen. These findings have led to a new taphonomic model that is discussed in chapter 6 of this thesis.

It is a main focus of this thesis to investigate the preconditions and taphonomic processes that led to the genesis of this fossil deposit. During the investigations on the material is arose that mainly the Neoptera of the pterygote insects show special types of preservation patterns that led to new insights on the taphonomy of the Lagerstätte.

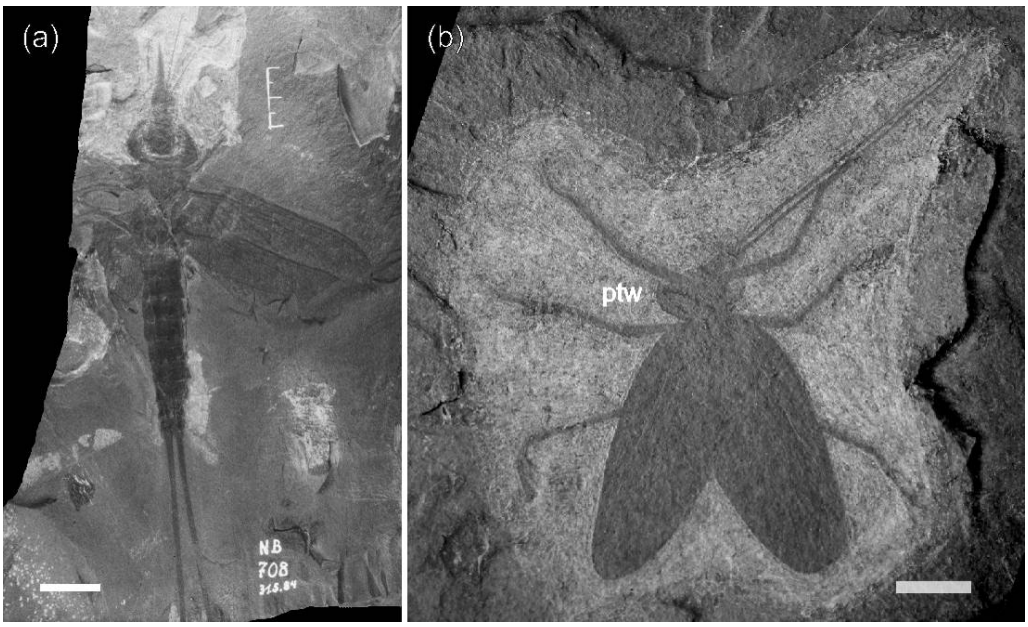


Fig. 6: Examples of characteristic preservation types in "Palaeoptera" and Neoptera from Hagen-Vorhalle. **(a)** "Palaeoptera" species *Homoioptera vorhallensis* BRAUCKMANN & KOCH, 1982 (Palaeodictyoptera: Homoiopteridae; specimen WMf.N P.27205) with abdomen, long cerci and head with appendages. Photograph by L. Koch. **(b)** Neoptera species *Kochopteron hoffmannorum* BRAUCKMANN, 1984 (basal Neoptera: ?Cacurgidae; specimen WMf.N P.26093 pos.) with long legs, head, filiform antennae, prothoracic winglets (ptw) and meso- and metathoracic wings in overlapping V-like resting position. Note the complete lack of an abdomen. Modified after ILGER & BRAUCKMANN (2008). Scale bars: 10 mm.

3 Material and methods

3.1 Techniques and equipment

Investigations were done using a Euromex ZT-45 zoom trinocular with an attached camera tube. Objects were illuminated with a Euromex EK-1 cold light lamp with polarizing filters to minimize reflections on clay minerals, mica layers, and other kind of reflecting surfaces. Imaging conditions for photo documentation were optimized by varying illumination levels and angles with polarized and non-polarized light. Additionally, specimens were lighted with ultraviolet light at two distinct wavelengths (λ_{UV1} = 254 nm; λ_{UV2} = 366 nm) using a Raytech LS-4CB fluorescent tube.

Photographs were taken by using a Canon EOS D60 digital reflex camera fitted with marco lens Canon EF 50mm f/2.5 Compact-Macro, a Canon PowerShot A470 digital point-and-shoot camera with Super Macro function and a Medion Life X47050 1080p digital camcorder with macro function.

Cameras were stabilized and elevated by a Velbon Sherpa 600R tripod. For high magnifications EOS D60 was attached to the tube of the trinocular. To prevent camera shake a Canon Remote Switch RS-80N3 was used instead of shutter button. Additionally to minimize shakes caused by the vibrations of shutter action the mirror lockup was enabled in the custom functions settings.

Digital images were edited using the computer programs ImageJ 1.41o, Corel PHOTO-PAINT 12, CorelDRAW 12, and GIMP 2.6.8. White balance was manually referenced to middle gray (reflectivity: 17.8%) by using a Mennon gray card.

Drawings were produced with the aid of a Euromex MIC 418 bypass prism attached to the trinocular eyepiece or directly on printed images. They were produced considering both the print and counter print in combination. Photographs of the two corresponding prints were digitally superimposed by mirroring and adjusting.

Some representative specimens were analyzed using a Keyence VHX-600 digital microscope to visualize prodissoconch surfaces in detail (2D and 3D).

For sub-visual investigations the scanning electron microscope (SEM) ISI ABT-55 equipped with an associated energy-dispersive X-ray spectroscopy unit (EDX) for elemental analysis was used. Samples were vacuum metalized with gold using a Cressington “cool” Sputter Coater 108auto. Low temperatures during metalizing ($T \approx$ 298–303 K) averted unwanted alterations e.g. of clay minerals and their structure.

Measurements of the specimens were done by the use of either a digital measuring gauge (scale-reading precision: ~0,01 mm) or by dint of the ImageJ 1.41o computer program. For this purpose a known distance within a photograph was referenced to the number of pixels, the pixel aspect ratio and the used unit of length. Subsequently the program is able to make any kind of measures of distance, length/width, and area.

3.2 Re-deformation

Intensive and dynamic tectonic processes that took place since the last >310 million years have deformed the entire sediment body (see chapter 2.5) of the Vorhalle Formation and also the fossils embedded in the rocks. In most cases there is even more than one generation of schistosity distinguishable. This caused an occasionally very pronounced distortion of the fossilized organisms. In most cases deformation remains unnoticed during paleontological research because there is no un-deformed reference object. Only in a very few specimens it is directly visible. An example has been described for *Zessinella siope* BRAUCKMANN, 1988 from the same locality. In this specimen one wing is abrupt, rotated and embedded perpendicularly to the other wings by taphonomic processes. As the wings were exposed to tectonic stress and strain from different angles they were deformed at different amounts.

Apart from this unique specimen there were no landmarks for the magnitude and orientation of tectonic deterioration to the fossils at all. At best it was known that the objects were deformed but it was impossible to reconstruct them completely un-deformed. But when wing measurements and venation patterns of different specimens should be compared to each other it is absolutely necessary to work with un-deformed fossils to ensure reproducibility. Especially when the variation of anatomical features is discussed this aspect becomes fundamentally significant.

Many of the Neoptera are associated with shells of ammonoids on the same plate. These cephalopods are abundant in the Vorhalle beds and occur all over the sediment layers. Mostly they can be allocated to different ontogenetic stages of *Bilinguites metabilinguis* (see chapter 2.4.1 and Figure 3) As their shells represent a planar approximated logarithmical spiral it can easily be characterized by mathematical methods. Not more than 19.5% (n = 41) of all positive and negative prints reviewed bear such cephalopod shell feasible for re-deformation.

The regular inner and outer windings were reconstructed and the radii of the shell (umbilicus–periphery) were measured in discrete pitches of 10° each incipient near the shell's aperture. Measurements were plotted in an MS Excel work sheet and after a whole circuit of 37 steps (0°, 10°, 20° ... 360°) the deformation factor D is assessed by dividing each radius r by the radius 0.25 circuit (i.e. $\alpha = 90°$) further:

$$D_n = r_n / r_{n+90°}. \qquad (1)$$

The resulting data were plotted in a diagram (Fig. 7). Apexes of the sinuous graph represent the direction of maximum elongation of the fossil whereas minima represent the direction of maximum constriction.

Additionally the mean deformation factor μD of the entire fossil was appointed as the arithmetic mean value from one extremum to another (either from D_{min1} to D_{min2} or from D_{max1} to D_{max2}):

$$\mu D = (D_1 + D_2 + ... + D_n) / n. \qquad (2)$$

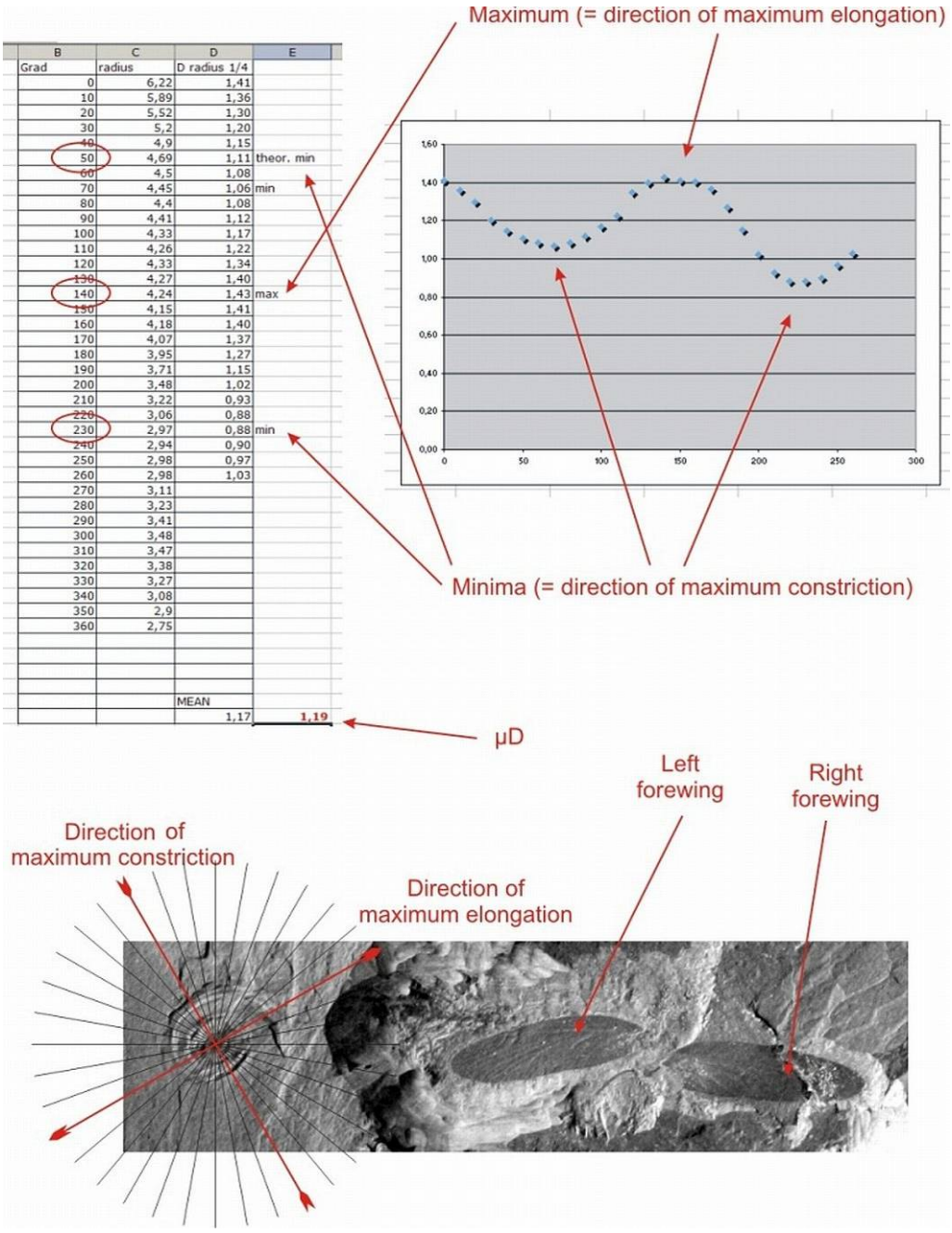
Hitherto 41 shells of ammonoids met the requirements and were included in the re-deformation analysis. The average value of μD and its standard deviation $\sigma_{\mu D}$ was determined:

$$\mu D = 1.21 \pm 0.093 \ (n = 41). \qquad (3)$$

Due to the high variability of concurrence and influences of sediment lamination, stratification, schistosity and the orientation of the fossils and preservation, the re-deformation factor has to be determined for each specimen separately. The resulting extremal values were: $\mu D_{max} = 1.47$, $\mu D_{min} = 0.94$. When the deformation factors of the ammonoid shells are known the associated insect fossil can be re-deformed; the object is compressed by the value of elongation and elongated by the value of compression. An exemplarily workflow can be found in Figure 7.

The resulting re-deformed reconstruction represents the proportions of the living insect and can be compared with other re-deformed specimens for studies of morphological variability.

Even if the shell does not lie exactly on the same lamina of the stratified siltstone this method can be used—with reservations—for re-deformation. The tectonic regime does not differ significantly over a vertical distance of a few millimeters and so stress and strain values and orientation can be assumed to be more or less equal in tight adjacent layers. But it can differ significantly in the case of bigger intervals up to centimeters or more. Therefore such specimens were not included in re-deformation processes.



Grad	radius	D radius 1/4	
0	6,22	1,41	
10	5,89	1,36	
20	5,52	1,30	
30	5,2	1,20	
40	4,9	1,15	
50	4,69	1,11	theor. min
60	4,5	1,08	
70	4,45	1,06	min
80	4,4	1,08	
90	4,41	1,12	
100	4,33	1,17	
110	4,26	1,22	
120	4,33	1,34	
130	4,27	1,40	
140	4,24	1,43	max
150	4,15	1,41	
160	4,18	1,40	
170	4,07	1,37	
180	3,95	1,27	
190	3,71	1,15	
200	3,48	1,02	
210	3,22	0,93	
220	3,06	0,88	
230	2,97	0,88	min
240	2,94	0,90	
250	2,98	0,97	
260	2,98	1,03	
270	3,11		
280	3,23		
290	3,41		
300	3,48		
310	3,47		
320	3,38		
330	3,27		
340	3,08		
350	2,9		
360	2,75		
		MEAN	
		1,17	1,19

Fig. 7: Exemplarily workflow of the Re-deformation process as executed with appropriate material form Hagen-Vorhalle.

3.3 Material

3.3.1 Hagen-Vorhalle

The complete material from Hagen-Vorhalle is deposited in the LWL-Museum für Naturkunde, Westfälisches Landesmuseum mit Planetarium in Münster (Germany). The specimens originated from both an official excavation campaign (1990–1997) by the museum (see chapter 2.2) and from private collectors who have since donated them to the museum. For investigation after a first examination on site the complete Neoptera material was brought to Clausthal-Zellerfeld. This was done step by step in some charges due to the high number of specimens (n > 210) and the size of some plates (up to 60 cm is diameter).

Preparation was done in Münster (SCHÖLLMANN 2005) by local experts. The work on this delicate material requires a high level of operating experience. Some specimens from the Münster collection were subsequently re-prepared for public exhibitions in the LWL-Museum (ILGER & BRAUCKMANN 2008). Since that time they had not been under afresh scientific investigation. Investigation of the specimens led to recovery of some spectacular new characters (see chapter 5.1).

3.3.2 Küchenberg locality near Fröndenberg

In October 2010 the private collector H. Bech brought to the author's attention a number of fossil insects (n = 10) which were collected by herself and G. Sommer from 1991 to 1997 in the abandoned Küchenberg quarry (N 51° 28.80', E 007° 44.43') near Fröndenberg/Ruhr (Germany). All specimens are preserved both with positive and negative prints (indicated as "a" and "b", respectively, as already interpreted by the collectors).

This material is considered to be of extraordinary importance as is comes from a new Lagerstätte that has not yet been investigated in detail. First reports of the deposit were given by (SCHULTKA 1995) who also mentioned one isolated specimen (all four wings and one isolated leg) of *Kemperala hagenensis* which also occurs in Hagen-Vorhalle. This specimen was exhibited in the local museum for some years. The other specimens were not considered in any publications or paleoentomological investigations so far. Interpretations of the new Lagerstätte, its relation to Hagen-Vorhalle and the systematic paleontology of the specimens is presented in chapter 7 of this work.

The complete material has been transported to Clausthal-Zellerfeld and preliminarily stored in the collection of the Institut für Geologie und Paläontologie, Abteilung für Paläontologie, Clausthal University of Technology in Clausthal-Zellerfeld (Germany). After the research project has come to an end it will either remain there or will be stored in the collection of the

Naturkundemuseum Berlin as most of the other material from Fröndenberg (mostly plant remains) is already there and still under paleobotanical investigation.

3.3.3 Other localities

Specimens of basal Neoptera of comparable age—although stratigraphically slightly younger—are known from the Upper Silesian Coal Basin of the Czech Republic and Poland. They mainly come from two Lagerstätten (see PROKOP & NEL 2007; PROKOP et al. in press) each on one side of the border.

The one on the Czech part of the basin is near Horní Suchá (formerly German Obersuchau; Polish Sucha Górna) at approx. N 49° 57.85', E 018° 37.12' and ~280 m a.s.l. It can be seen as a "classical" locaction for the investigation on early Neoptera as the material of KUKALOVÁ (1958) came from here.

The other location on the Polish part is the Porąbka-Klimontów coal mine in Sosnowiec (formerly German Sosnowitz) at approx. N 50° 17.00', E 019° 08.00' and ~330 m a.s.l. It is located about 100 km northeast of Horní Suchá.

The material is deposited at the Department of Zoology, Division of Entomology, Charles University in Prague (Czech Republic) and the Natural History Museum of the Institute of Systematics and Evolution of Animals, Polish Academy of Science in Kraków (Poland). The material was not investigated by the author in person but Polish and Czech colleagues provided high resolution photographs and detailed descriptions.

3.4 Nomenclature of insect wing venation pattern

The nomenclature of wing venation follows KUKALOVÁ-PECK & WILLMANN (1990), KUKALOVÁ-PECK (1991) and KUKALOVÁ-PECK & BRAUCKMANN (1992). Main vein terminology corresponds to this scheme:

ScP– ..... Subcosta posterior;
R ..... stem of Radius,
RA+ ..... Radius anterior,
RP– ..... Radius posterior;
M ..... stem of Media,
MA+ ..... Media anterior,
MP– ..... Media posterior;
Cu ..... stem of Cubitus,
CuA+ ..... Cubitus anterior,

CuP– ..... Cubitus posterior;
A ..... Anal veins in general,
AA+AP ..... complex of Anal veins (branches both of Analis anterior and posterior),
AA+ ..... Analis anterior,
AP– ..... Analis posterior.

Additional subscripts index the number of subsequent terminal branches: e.g. RP_1– = most anterior (distal) branch of RP–.

Other significant wing characters:

arc ..... arculus (= strong cross-vein between CuA+ and MP–),
cmf ..... cubito-median fold (= convex fold between CuA+ and MP–, mostly very close and sub-parallel to CuA_1+). – Remark: Usual sequence in wing descriptions is from anterior to posterior, so the term would rather be "medio-cubital fold" (mcf). In this thesis the authors follows the nomenclature used by NEL et al. (2007) for the description of *Westphalomerope maryvonneae* for better comparability.

Attached signs "plus" (+) and "minus" (–) indicate the corrugation of the wing; i.e.: + = convex (in figures: above plane of projection), – = concave (in figures: below plane of projection) for wing viewed in dorsal aspect. This "wing topography" is called the corrugation of the wing (e.g. KUKALOVÁ-PECK 1983; 1991). From the phylogenetic point of view wing main veins are homologue characters. According to this the anterior main branch of a vein stem is always superior ("positive") and the posterior main branch always inferior (negative") of the wing average wing plane. This alternating appearance has positive effects on flight behavior and aerodynamic properties of the wing (e.g. REES 1975; XUE et al. 2011) and likewise mechanical stabilization of bending and torsional deformation in flight.

4 The "Palaeoptera"–Neoptera problem

4.1 The basal Pterygota polytomy

In this work the term "Palaeoptera" is used in a strictly descriptive meaning. The group is outlined by the similar morphology of constituent taxa in contrast to the Neoptera. "Palaeoptera" are Pterygota which are (primary) not able to fold their wings across their abdomen and their articulation plates are not fused. Most probably they are not monophyletic. In general, the early evolution of Pterygota is a controversial subject. The "European/American school" (e.g. GRIMALDI & ENGEL 2005 and further references therein) regards the "Palaeoptera" as more primitive than the Neoptera. The latter are Pterygota which are able to fold their wings across the abdomen by a fused band of articulation plates: They have a turnable axillare 3 (i.e. the 3rd axillary sclerite, one of several plates that articulate the wing base at the meso- and metathorax; see Fig. 8) with an attached muscle. A contraction of this muscle causes the turning of the sclerite as well as the folding of the wing and its moving into the backward resting position.

Contrary to this interpretation, the "Russian school" (e.g. RASNITSYN & QUICKE 2002 and further references therein) regards the early Neoptera as more primitive and the palaeopterous wing articulation as more derived and secondary.

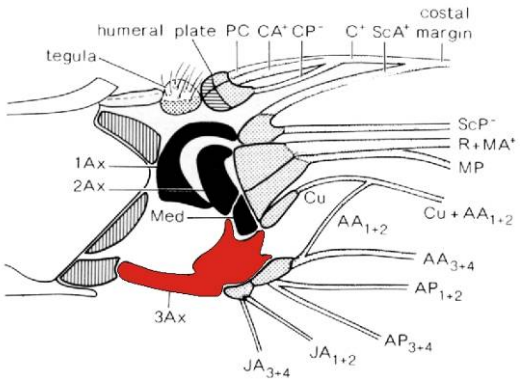


Fig. 8: Diagrammatic pattern of wing base articulation plates in Neoptera. Venation nomenclature corresponds to the scheme in chapter 3.4 of this thesis. Additionally: PC = Precosta, C = stem of Costa, CA = Costa anterior, CP = Costa posterior, JA = Jugalis anterior, Med = medial plate, 1Ax, 2Ax, 3Ax = 1st, 2nd, and 3rd axillary plates. The turnable axillare 3 is highlighted in red. Modified after KUKALOVÁ-PECK (1991).

In this thesis the working hypothesis of the author is that the basal Neoptera from Hagen-Vorhalle had a turnable axillare 3 and can consequently be attributed to the Neoptera. This assumption is mainly based on the V-like wing folding pattern over the abdomen. It is presumed that this motion is so unique that the most parsimonious interpretation is a singular development of this character ("wing folding" of Recent Zygoptera SÉLYS-LONGCHAMPS in SÉLYS-LONGCHAMPS & HAGEN, 1854 is a completely different type that works without a turnable axillare 3).

If this hypothesis is true, the basal Neoptera from Hagen-Vorhalle can either (i) belong to the stem group of all Neoptera, (ii) belong to the stem group of one of their subgroups (for example the Plecoptera BURMEISTER, 1839 as presumed most basal group of the Neoptera), or (iii) form an adelphotaxon (= sister group) of one of their subgroups.

So far, until all of these questions have been answered, there are three competing hypotheses to explain the basal Pterygota polytomy. A recent synopsis of the three hypotheses with data from morphology, paleontology, recent entomology and molecular analyses is given by KLASS (2007; 2009) and SIMON et al. (2009). Each hypothesis is discussed briefly in the following sections.

4.2 Metapterygota hypothesis

Ephemeroptera + Metapterygota (= Odonata + Neoptera)

According to this hypothesis the Ephemeroptera HYATT & ARMS, 1890 are an adelphotaxon to the Odonata FABRICIUS, 1793 and Neoptera, summarized to Metapterygota BÖRNER (1909) (Fig. 9). STANICZEK (2000) has shown that the morphology of the mandibles contributes synapomorphies for this hypothesis. Unfortunately mouth parts are not well preserved in the basal Neoptera from Hagen-Vorhalle.

Other arguments for this hypothesis come from the individual development from the nymphal instars to the imago. The existence of a subimaginal stage which is also able to fly is unique in Ephemeroptera—also in Recent mayflies. Furthermore the arrangement of tracheae stems, nerve tracts, genitalia and the heart have been used to confirm this approach, (see KLASS 2007 for overview and further references therein).

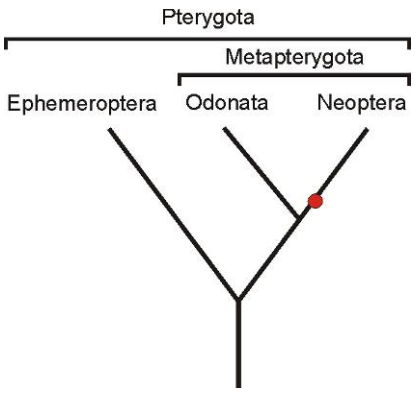


Fig. 9: Phylogram illustrating the relationships of basal Pterygota according to the Metapterygota hypothesis. Red circle indicates position of basal Neoptera.

4.3 Chiastomyaria hypothesis

Odonata + Chiastomyaria (= Opisthoptera sensu AX (1999)) (= Ephemeroptera + Neoptera)

This hypothesis may be less probable, but it should be likewise mentioned with regard to the interpretation of the basal Neoptera. In this case, they should be derived from an "Ephemeroptera ground type" (Fig. 10), and the resting mode of the wings of Ephemeroptera must be regarded as plesiomophic.

A main argument is the arrangement and insertion of muscles in the flight apparatus. This is unique in Odonata. But—on the other hand—this character is highly affected by the mode of life and flying behavior. Odonata (as vividly visible in Recent dragonflies) are highly advanced high-speed fliers which may presuppose a special adapted propulsion system.

The main problem in the discussion about this hypothesis is the direction of reading the characters; i.e. the polarity.

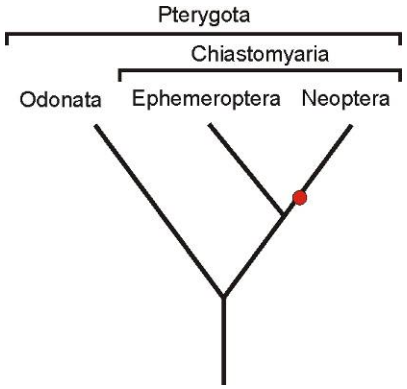


Fig. 10: Phylogram illustrating the relationships of basal Pterygota according to the Chiastomyaria hypothesis. Red circle indicates position of basal Neoptera.

4.4 Palaeoptera hypothesis

Palaeoptera (= Odonata + Ephemeroptera) + Neoptera

In this hypothesis Palaeoptera MARTYNOV, 1923 are seen to be monophyletic (Fig. 11; this is the reason why the term is not set in quotation marks in this paragraph). The hypothesis is probably confirmed by molecular data (e.g. HOVMÖLLER et al. 2002; recent overview in KLASS 2007; 2009). Furthermore a primary paired penis in male individuals is argued to be a synapomorphy that divides the Neoptera from the Palaeoptera. Another important character in this discussion is the specifications of the mouthpart appendages.

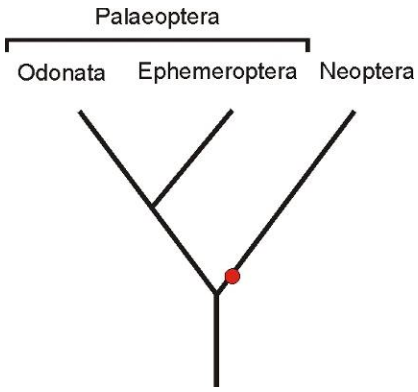


Fig. 11: Phylogram illustrating the relationships of basal Pterygota according to the Palaeoptera hypothesis. Red circle indicates position of basal Neoptera.

Part II

Results

5 Systematic paleontology of Hagen-Vorhalle

5.1 New characters in known species

5.1.1 Prothoracic winglets in basal Neoptera

Lateral winglike prolongations of the prothorax in early Pterygota are still controversial. Many palaeoentomologists (e.g. KUKALOVÁ-PECK 1991, and further references therein) interpret them as true prothoracic winglets. On the other hand others (e.g. RASNITSYN & QUICKE 2002 and further references therein) consider them as pronotal lobes and to be secondary.

CARPENTER (1992: 27; chapter about the order Palaeodictyoptera) adopted a moderate view with an undecided definition as "a pair of lateral winglike lobes, usually membranous and commonly with veinlike supports." A similar approach was taken by GRIMALDI & ENGEL (2005).

These vein-like structures can be found in well preserved specimens and resemble the main venation pattern of the meso- and metathoracic wings. This was vividly shown by BRAUCKMANN (1991b) and BRAUCKMANN & HERD (2007) for *Homoioptera vorhallensis*, a Palaeodictyoptera from Hagen-Vorhalle (Fig. 6a on p. 18). Also the typical divergence of veins into anterior and posterior main branches can be found. Especially a subcircular wing from the Piesberg quarry near Osnabrück (Pennsylvanian: Westphalian D; western Germany) shows this very well (BRAUCKMANN & HERD 2007). It can be allocated either to Palaeodictyoptera or Ephemeroptera.

In a recently published paper by ILGER & BRAUCKMANN (2008) the occurrence of prothoracic winglets in a single specimen of *Kochopteron hoffmannorum* BRAUCKMANN, 1984 (specimen WMf.N P.26093 pos.) from Hagen-Vorhalle has been described for the first time (Fig. 6b on p. 18). Moreover it provides the first and only direct evidence for wing like appendages on the prothorax in the "basal Neoptera". The new anatomical details became visible after a second preparation during the course of an exhibition by the LWL-Museum für Naturkunde in Münster.

So far former reconstructions of Late Carboniferous Neoptera show in fact the presumed prothoracic winglets—independent of their evolutionary meaning. But they have never been proved before. Only one single specimen of *Heterologopsis ruhrensis* (i.e. the holotype; specimen WMf.N P.22459A/B) shows a very special damaged matrix of the embedding rock which surrounds the fossil corpus that allows the presumption that there must have been such winglets.

The prothoracic winglets of *K. hoffmannorum* were found in situ. One of them is slightly shifted a few millimeters which may be indicative of (at least marginal) movability. This supports the hypothesis that these organs are real winglets and not just pronotal lobes as they occur in Zygentoma (for argumentation see HASENFUSS 2002, YANOVIAK et al. 2009). Likewise in light of the proven wing-like venation of other prothoracic winglets by BRAUCKMANN (1991) and BRAUCKMANN & HERD (2007) they can be assumed to be real winglets and not pronotal lobes (see also discussion in ILGER & BRAUCKMANN 2008). Unfortunately, the preservation of the specimen

(and all other specimens of *K. hoffmannorum*) does not allow identification of such a venation pattern. Nevertheless these organs can be assumed to be serially homologous to the meso- and metathoracic wings.

A comparison of the prothoracic winglets found in *K. hoffmannorum* with found in other taxa (e.g. Palaeodictyoptera) indicate that the basal Neoptera ones were more wing-like than those in ancient "Palaeoptera". Their shape was not sub-circular, but elongated with a rounded apex. Furthermore their base was narrower and not as broad as the whole prothorax.

The occurrence of prothoracic winglets is interpreted to be strongly plesiomorphic and probably it is even a part of the Pterygota groundplan pattern. After a reduction of the prothoracic wing-like appendages some groups have evolved functional substituting organs in a convergent evolution. This led to the development of pronotal lobes e.g. of the Blattaria LATREILLE, 1810 and others. Mechanically and functionally they may have worked in a very similar way—probably a mode of flight stabilization.

From an evolutionary development point of view even a few simple mutations in some genes allow arthropods to make drastic changes in their number of arrangements of segments and appendages (e.g. wings, legs etc.; see e.g. JOCKUSCH & OBER 2004, ANGELINI & KAUFMAN 2005, NIWA et al. 2010). This has empirically been proven in the case of Hox genes in *Drosophila* Fabricius, 1787 and can lead to drastic phenotypic differences; as may have happened in the loss or reduction of the "first pair of wings" of ancient Pterygota.

Unfortunately, there are no further details within the winglet membrane (like venation and/or archedictyon) visible. This is possibly due to their having been preserved as thin graphitic layers.

5.1.2 Abdomens and ovipositors in female basal Neoptera

Basal Neoptera from Hagen-Vorhalle show a very special preservation pattern, virtually all of them lack an abdomen. This fact is not true for all Pterygota from the Lagerstätte: "Palaeoptera" usually show a complete preserved abdomen inclusive of attached cerci and genital appendages (both in male and female individuals). A new taphonomic model to explain this circumstance can be found in chapter 6 of this thesis, where more facts and descriptions can also be found.

Of the complete Neoptera material from Hagen-Vorhalle only three specimens of were discovered that exhibit an ovipositor: specimens WMfN. P.20661 (both positive and negative print), P.22596A/B (both positive (A) and negative print (B)), and P.31712 (only positive print). Only one of these individuals (P.20661) shows a shadowy imprint of the abdomen on the positive print. The other ovipositors are embedded in situ but the abdomen itself cannot be identified in the material (Fig. 12). One of the specimens (P.22596A/B) is the holotype of the genus and species. Formerly the ovipositor was interpreted as a broken part of a leg but a new re-preparation by the LWL-Museum in Münster revealed the true meaning.

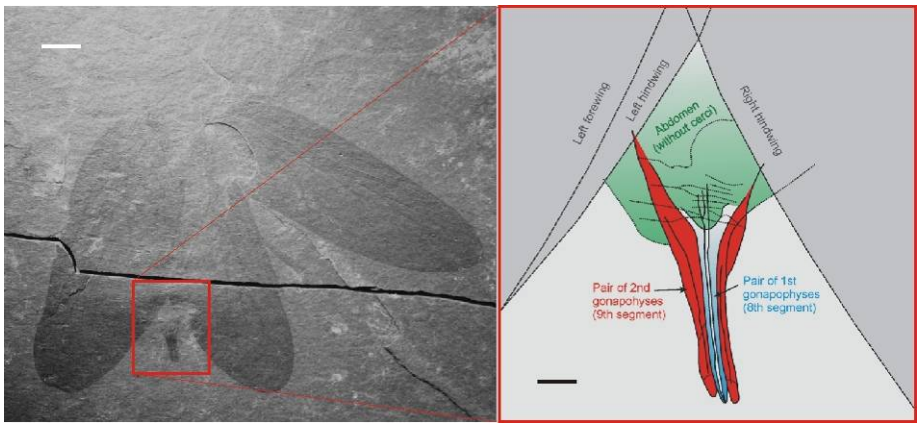


Fig. 12: Female specimen of *Kochopteron hoffmannorum* BRAUCKMANN, 1984 (specimen WMf.N P.31712, positive print) showing a well preserved ovipositor. **(a)** Photograph; Scale bar: 5 mm. **(b)** Interpretative drawing; position and size of the abdomen (green) is postulated and not well-preserved in the material; Scale bar: 1 mm.

This thesis is the first report including pictures and interpretative drawings of such female genital organs in basal Neoptera. However, the material is still under intensive investigation that has to be continued beyond this work. The investigation is part of a current extended DFG research project (BR 1253/4-2) in co-operation with the paleoentomological working group of the Charles University in Prague (Czech Republic) and will end in May 2012. The aim of the project is to figure out the morphological characteristics and phylogenetic implications of the ovipositors within the phylogram of basal Pterygota. This will be a "hotspot focus" of our further work and it could lead to complete new assumptions for early Pterygota evolutionary pathways. Therefore only a descriptive introduction to the ovipositors is given in this thesis.

The three female specimen exhibit clearly visible (i.e. well sclerotizied) lacinial ovipositors. In general the abdomen seems to be rather short—much shorter than assumed in previous reconstructions like those of BRAUCKMANN et al. (2007). Since there are no cerci visible, it is supposed that they were either completely lacking or at least strongly reduced and very short. This could have functional reasons, e.g. to enable agile flight movements. A light, thin-skinned and soft abdomen that is furthermore reduced in length may have been beneficial for lift-off and flight behaviour. – These argumentations may lead to the conclusion that basal Neoptera were much better active fliers than Late Carboniferous "Palaeoptera" which were mostly gliders (see also chapter 5.1.4 about beginning cell formation in basal Neoptera wings).

Under polarized/unpolarized incident light at diverse angles gonapophyses of the 9th and 8th abdominal segment (S8 and S9) were found. They appear in pairs; thus four components can be distinguished: The anterior pair of gonapophyses (of the 8th abdominal segment) is preserved in ventral position, the posterior pair (of the 9th abdominal segment) in dorsal position. Among the elongate and sheath-like gonapophyses of the 8th abdominal segment there is a chasm-like space formed in between.

The abdomens are not well preserved, as is the case in all other Neoptera from Hagen-Vorhalle. But in a single case (specimen WMf.N P.20661) it can be slightly seen as a thin shadow between ovipositor and crossed hind wings. This corresponds to the (most probably in situ position) of the ovipositors in the other specimens and permits conclusions concerning the total length of the abdomen and its possible appendages. Elongate cerci or similar structures seem to be completely absent. They might simply not have been preserved, but since there are other delicate structures well preserved in this specimen it is assumed that they may be strongly reduced in this species.

The occurrence of an ovipositor at the 8th and 9th abdominal segment is an autapomorphy of the Ectognatha STUMMER-TAUNFELS, 1891. In the Dicondylia HENNIG, 1953 a big gonangulum at the basis of the ovipositor is developed. Thus the gonapophyses were likely movable against each other. This was obviously also true in the Paoliidae. On the level of the basal Neoptera these characters are of course plesiomorphic.

The ovipositor of *K. hoffmannorum* was even and slender. It resembles those ones of the Orthoptera OLIVIER, 1789, but a serration (a typical boring structure) is lacking. Thus it may have been used for egg deposition in a soft soil (e.g. mud) or shallow submersed substrates (e.g. stipes). Nevertheless, the similarity of the ovipositor in *K. hoffamnnorum* and the one in Orthoptera is remarkable. Further investigation will show whether this indicates a close relationship or is a plesiomorphy near the groundplan without apomorphic specialisations. These questions can only be resolved by the materials from Hagen-Vorhalle because this is the one and only site worldwide to include completely preserved specimens.

5.1.3 Legs with tarsi and claws

Former publications on the basal Neoptera from Hagen-Vorhalle mention or figure the presence of legs (coxa + trochanter + femur + tibia) and tarsi but none gives an intensive description of this anatomical feature. Herein the first findings are presented.

As in the case of the ovipositors and abdomens (see preceding chapter 5.1.2) these characters are the focus of work of a current extended DFG research project (BR 1253/4-2) in co-operation with the Charles University in Prague.

The legs of the Neoptera from Hagen-Vorhalle are often embedded in situ. The prothoracic pair is orientated forward and lies sometimes sub-parallel to the antennae. The meso- and metathoracic legs are directed backward and are in part covered by the wings in resting position. Due to this position the trochanter, coxa and the articulation to the thorax are not visible. Femur and tibia are in general well preserved and strong. Spines or similar structures are not visible. The tarsus is mostly disarticulated and lost during taphonomic processes. Only a few samples show a complete tarsus with all tarsomeres (Fig. 13).

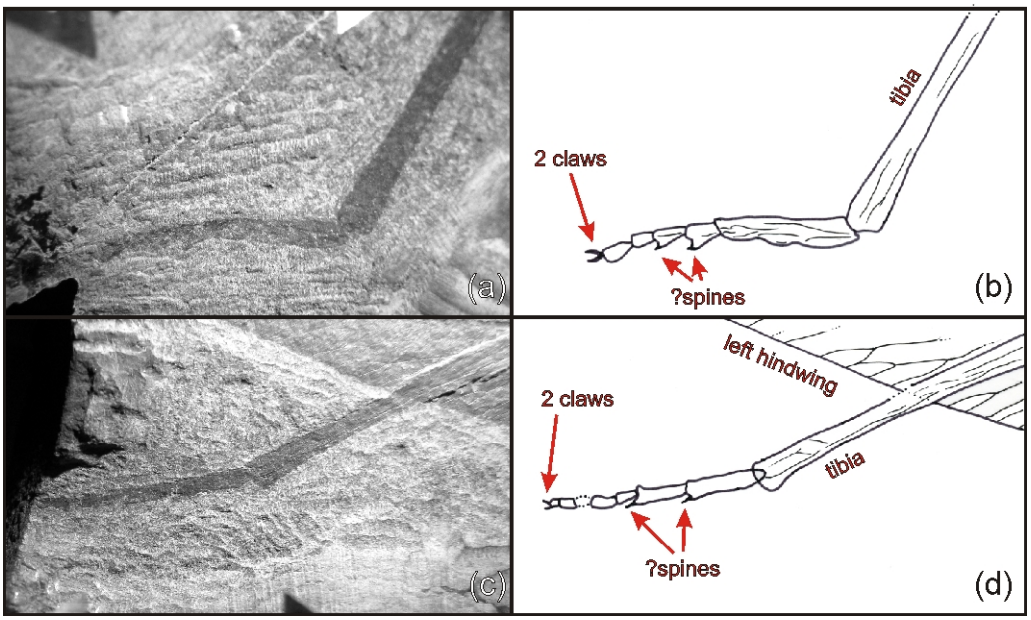


Fig. 13: Detail of *Kemperala hagenensis* BRAUCKMANN, 1984 (specimen WMf.N P.25834) showing a complete tarsus with five tarsomeres. **(a)–(b)** Photograph and interpretative drawing of the left mesothoracic leg. **(c)—(d)** Photograph and interpretative drawing of the right metathoracic leg.

The best preserved specimen so far is an exemplar of *Kemperala hagenensis* (specimen WMf.N P.25834). The tarsus consists of 5 tarsomeres (t_1–t_5). The pretarsus (t_5) bears two claws. Both are plesiomorphic characters. An apomorphy is the enlargement of some tarsomeres and their spines: At the left mesothoracic leg (Fig. 13a–b) the first tarsomere (t_1) is about 5.5 times longer than each of the others, and has a slightly undulated hind rim and no spines. Tarsomeres t_2 and t_3 are marginally enlarged in comparison to the other tarsomeres and bear a single spine. At the right metathoracic leg (Fig. 13c–d) the first two tarsomeres bear a single spine and are longer than the other ones: t_1 is about four times longer and t_2 is about triply longer than each of t_3, t_4, and t_5.

In general the legs of *K. hagenensis* seem to be quite plesiomorph but show some specializations in the tarsus morphology. In none of the basal Neoptera species *K. hagenensis*, *H. rasnitsyni*, and *K. hoffmannorum* can a patella be proven. Only the few specimens of *Heterologopsis ruhrensis* may have a patella as e.g. figured by BRAUCKMANN et al. (2003: 47) for the holotype.

During the ongoing investigation in the extended application the legs of other specimens and taxa should be examined to complete the features.

5.1.4 Tendency to beginning cell formation

By attentive revision of the complete material a new parameter of the wing venation pattern has been discovered. In a few specimens, most importantly of *Holasicia rasnitsyni*, the terminal branches of RP– and MP– show the tendency to fuse. The veins merge with each other some

millimetres or at the utmost ~0.5 cm before the wing edge. They can either run together to the edge or separate again and lead to the edge in two different branches. In the latter case they enclose a small cell.

Certainly they do not resemble real venation cells like modern insect groups do. But it seems to be a new variant in the venation pattern of the basal Neoptera that anticipates modern characters. It could also be an autapomorphy of the family Paoliidae.

So far it can be supposed that this beginning cell formation had a stabilizing function in flight. Since the basal Neoptera were advanced flyers the wings were more highly strained than in simple "Palaeodictryoptera-like" gliding and fluttering. Neopterous flight demands a high level of wing stabilization to prevent buckling and crippling of the stringer-like main veins.

Thus the cross veins may support the bracing of the archedictyon veinlets, eventually replacing them in higher derived groups.

A similar tendency leading from a finely woven archedictyon to a few cross-veins can be found in *Bechala sommeri* from the Küchenberg location (see chapter 7.3 and Fig. 30 on p. 73). It can s supposed that the Late Carboniferous was a period when higher maneuverability in Pterygota flight became an ecological advantage. As the winged insects became more and more diverse during the Carboniferous the pressure of competition also began to increase. Basal Neoptera may have had an advantage as their flight was much faster and more agile than in "Palaeoptera". This might be one reason why the first group became more successful in Earth history.

5.2 New species from Hagen-Vorhalle

5.2.1 Overview

With *Baryshnyala occulta* (Baryshnyalidae) a new small species from Hagen-Vorhalle is reported. It differs in its unique venation pattern and small size from all other Neoptera known from this Lagerstätte and other contemporaneous locations worldwide. With an estimated wing length of <10 mm it is by far the smallest species of Neoptera from Hagen-Vorhalle and is less than half as long as *Heterologopsis ruhrensis* (~25 mm). The specimen shows some relations to the earliest Holometabola and may date back the first appearance of holometaboly to the Namurian B (early Bashkirian: Marsdenian). The new species increases the paleo-biodiversity and span of inter-specific variability within the early Neoptera. It shows that very small and tiny specimens and species can easily be overlooked.

5.2.2 Systematics

Infraclass Neoptera MARTYNOV, 1923

Family Baryshnyalidae

Type (and only know) genus: *Baryshnyala*

Diagnosis. Wing small and well rounded, with the following venation pattern: (i) strong cross-vein between MP– and CuA+ in basal part of wing (arculus), (ii) pronounced convex fold between MP– and CuA+ (cubito-median fold), (iii) CuP– strongly convex, with 3 terminal branches, (iv) a number of straight cross-veins between main veins.

Genus *Baryshnyala*

Type (and only known) species: *Baryshnyala occulta*

Diagnosis: Very small (length <10 mm) and compact wing with well rounded apex. The venation pattern shows a combination of the following unique characters: (i) RP– branches far before reaching the mid-wing, (ii) well pronounced cubito-median fold, (iii) CuP_1– very strongly convex, (iv) posterior branches of MP– and CuA+ curved backwards (strongly convex), (v) no archedictyon but a number of cross-veins mainly in distal half of the wing.

Remarks: Despite the small size of the wing the regular shape precludes that it is a nymphal wing as it shows no kind of a typical strong backward flexion.

Etymology: The genus name is a combination of the Russian “барышня” [baryshnya] for young, unmarried woman and Latin “ala” for wing; gender feminine.

Baryshnyala occulta

Fig. 14a–b, 15a–f

Holotype: (and only known specimen): Specimen WMf.N P.212999, left metathoracic wing, with slightly damaged apex and lacking wing base. Stored in the collection of the LWL-Museum für Naturkunde, Westfälisches Landesmuseum mit Planetarium in Münster (Germany).

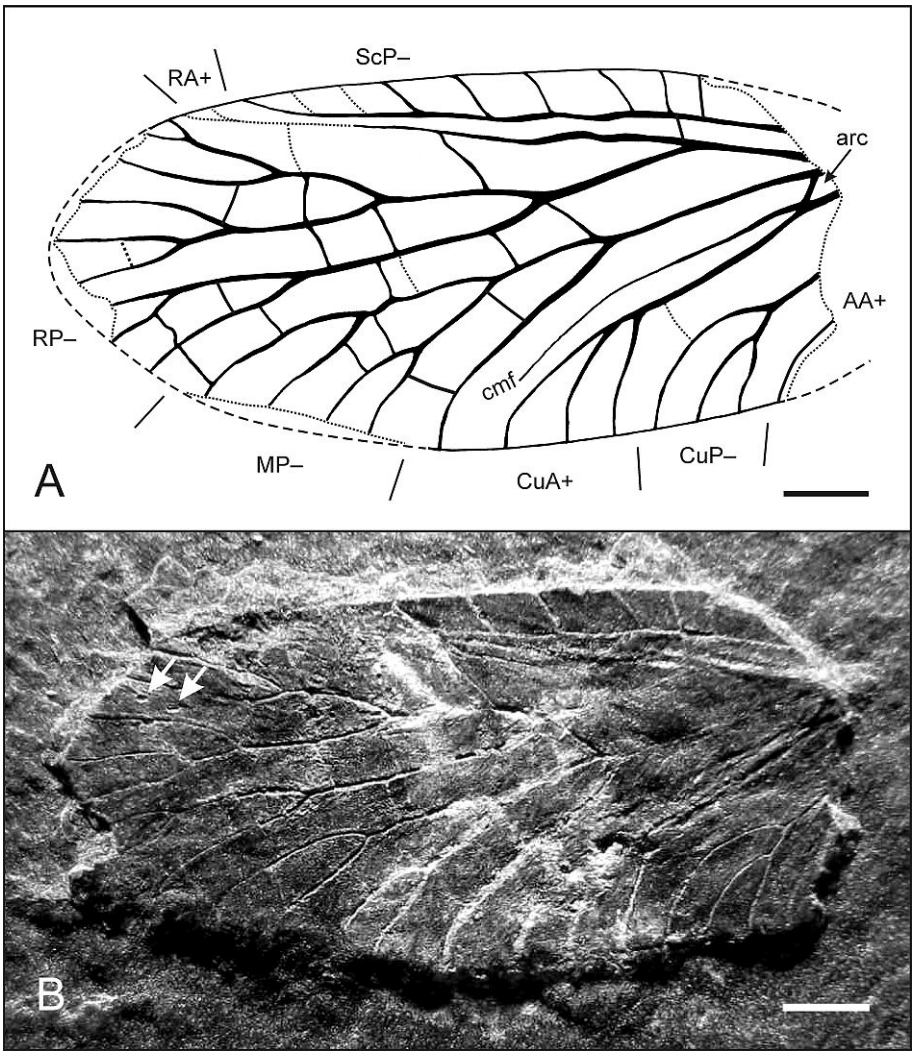


Fig. 14: *Baryshnyala occulta*; holotype, isolated left metathoracic wing (specimen WMf.NP.21299) **(a)** superimposed drawing with interpretation of the wing venation pattern; black arrow indicates arculus (arc), **(b)** photograph under polarized light; white arrows indicate attached bivalve prodissoconchs (see chapter 6 on taphonomy). Scale bars: 1 mm.

Type locality: Former brickyard quarry near Hagen-Vorhalle, North Rhine-Westphalia, Germany (topographic map 1 : 25,000, sheet no. 4610 Hagen/Westfalen; 51° 22.88'N; 007° 26.77'E; ~115 m a.s.l.).

Type stratum: Early Late Carboniferous (Early Pennsylvanian): early Bashkirian, late Namurian B, late Marsdenian, ammonoid zone R2c, Ziegelschiefer Formation.

Diagnosis: As for the genus (due to the temporarily monospecific status). Length ≥9.6 mm.

Preservation: The isolated wing is quite well preserved, though it lacks the proximal tenth with articulation and most of the anal area. Apical wing margin is also slightly damaged. The corrugation is easily discernible but flattened by diagenetic compression. The anterior

mid-wing is slightly damaged by preparation marks which obscure the exact reconstruction of terminal ScP– and RA+ branches—especially whether they do or do not fuse.

Also visible in the apical area (Fig. 14b), tiny prodissoconchs of young bivalves are attached to the dorsal wing membrane. These embryonic shells are common in basal Neoptera from Hagen-Vorhalle but are absent in all other Pterygota from the same locality. This has led to new interpretation of the taphonomy of the Lagerstätte. The model implies a stage of drifting along a pycnocline in a well stratified water body. During this period the corpses were affected by free-swimming bivalve larvae (see chapter 6).

Measurements: Preserved length: 8.7 mm; estimated length: ≥9.6 mm; maximum width (at most posterior branch of MP–): 4.2 mm. Approximated ratio length/width: ~2.3.

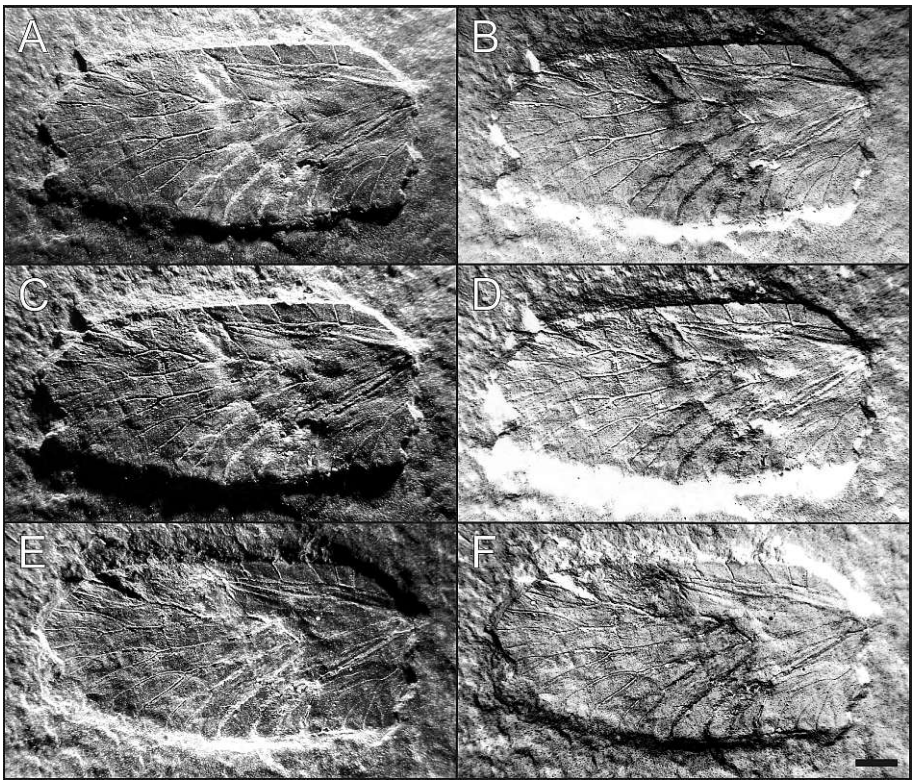


Fig. 15: *Baryshnyala occulta*; holotype, isolated left metathoracic wing (WMf.N P.21299);**(a)–(f)** One and the same wing in different illumination settings. Scale bar: 1 mm.

Description: There is only one isolated wing known. Due to its shape and the existence of a cubito-median fold it can be supposed it is a metathoracic wing (Fig. 14–15). Costal margin in mid-wing straight, apex well rounded. Costal area strongly pectinate with wide-standing cross-veins. ScP– simple and most likely reaching costal margin. R stem proximally thick and strong, branching in proximal quarter of wing length. RA+ simple and generally straight, terminal development not well preserved but probably reaching costal margin in distal fifth. RP– well and strongly developed, with 9 terminal branches. MP– strong, with 5 terminal branches, first branching clearly before mid-wing and fanning at basal third of wing length, posterior

branches strongly curved backwards at posterior wing margin. Strong arculus (= cross-vein between MP– and CuA+) present in proximal eighth of the wing. CuA+ slightly reduced, slightly concave in the middle part before branching, with 3 terminal branches, all very strongly curved backwards. Well developed and probably sclerotizied cubito-median fold (between MP– and CuA+) running close to CuA+, especially in the proximal part. CuP– with 3 terminal branches, CuP_1– very strongly convex. First AA+ straight. A number of thin and straight cross-veins mainly in the sectors of RP– and MP– and distal of mid-wing.

Etymology: Latin occultus, -a, -um (adjective) meaning arcane. The holotype specimen was stored for twenty years in the collection without being identified as a new species.

Discussion:

(a) Small basal Neoptera of the Late Carboniferous

Baryshnyala occulta can be easily separated from all other Neoptera from Hagen-Vorhalle by its very small size (length: ≥9.6 mm, width: 4.2 mm). In comparison to other wings within this group the specimen is about half as long as *Heterologopsis ruhrensis* (length: ~25 mm, width: ~8 mm). *Holasicia rasnitsyni* (length: 36 mm, width: 13 mm) and *Kochopteron hoffmannorum* (length: 41 mm, width: 13 mm) are distinctly larger, and *Kemperala hagenensis* (length: 61 mm, width: 22 mm) is by far the largest species of basal Neoptera from Hagen-Vorhalle (Fig. 16). *Baryshnyala occulta* fits very well in this set of proportions: all species show a tendency towards a length/width ration about 3 (l/w = 2.8 in *B. occulta*). *K. hagenensis* and *K. hoffmannorum* seem to vary mostly in the wing length whereas the width is more consistent. In contrast, the wings of *H. rasnitsyni* vary more in their width and less in length. The variation in *H. ruhrensis* and *B. occulta* is unknown because they are monotypic.

Further small Late Carboniferous (Pennsylvanian) basal Neoptera from localities in northwestern Germany and thus close to Hagen-Vorhalle are for example (arranged by their stratigraphical age):

(1) *Metropatorites kassenbergensis* KELLER, 1934 (ord. et fam. inc. sed.), Namurian C (Bashkirian: Yeadonian): preserved length: 9 mm, estimated total length: ~22 mm, preserved width: 5 mm, estimated maximal width: ~9 mm.
(2) *Micropalentomum minusculum* SCHMIDT, 1962 (Micropalentomidae), late Westphalian A (Bashkirian: Langsettian): length: ~3,5 mm [sic!], width: ~1 mm.
(3) *Eodelopterum priscum* SCHMIDT, 1962 (Miomoptera: Archaemiopteridae), early Westphalian B (late Bashkirian: Duckmantian): length: <5 mm, width: ~2.3 mm.

(4) *Heterologellus teichmuellerae* SCHMIDT, 1962 (Protophasmatidae), early Westphalian C (Moskovian: Bolsovian): length: ~18 mm, width: ~7 mm.

(5) *Controversala miomopteroides* BRAUCKMANN & HERD, 2005 (ord. et fam. inc. sed.), Westphalian D (late Moskovian): preserved length: 19 mm, estimated total length: ~20 mm, width: 8 mm.

Worldwide there are known many other small Neoptera from the Late Carboniferous and Permian. Especially Early Permian Protomeropidae Tillyard, 1926 are very small. For example *Westphalomerope maryvonneae* NEL et al., 2007 from the early Langsettian (Late Carboniferous: Bashkirian, Westphalian A) of France is half the size of *B. occulta*.

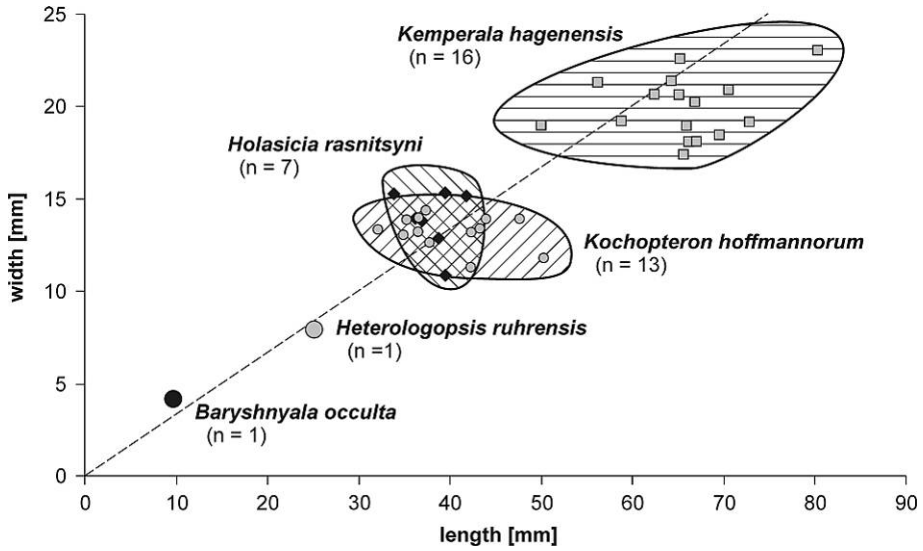


Fig. 17: Diagrammatic synopsis of wing proportions in basal Neoptera from Hagen-Vorhalle. *Baryshnyala occulta* fits very well in this set: all species show a tendency towards a length/width ration about 3 (dashed graph).

(b) Most ancient representative of Holometabola?

The probably earliest evidence for holometabolous insects is a metathoracic wing of *Westphalomerope maryvonneae*. As the authors correctly pointed out, Holometabola lack a distinct synapomorphy in their wing venation pattern. The allocation to Endopterygota SHARP, 1898 is done by attribution of *W. maryvonneae* to a subgroup of this clade, e.g. the family Protomeropidae. An adapted diagnosis of the family is given by SUKATSHEVA (1976). The two main characters are (terminology changed to the scheme used in the present paper): (i) a brace (= arculus) between CuA+ and MP–, and (ii) a heavily sclerotizied convex fold in front of CuA+ (= cubito-median fold). Such fold is not restricted to Holometabola but can also be found e.g. in

Evenka archaica RASNITSYN, 1977 which is probably close related to Paoliidae. Furthermore an arculus is also widespread and can be found in Paoliidae and other groups as well.

Both species, *B. occulta* and *W. maryvonneae*, share the following characters within the diagnosis by KUKALOVÁ-PECK & WILLMANN (1990; terminology here adapted): (i) narrow costal area, (ii) very narrow area between ScP– and RA+, (iii) arculus present (typical for Permian Protomeropidae but lacking in *W. maryvonneae*), (iv) well developed and prominent cubito-median fold, sub-parallel to $CuA_{(1)}$+, (v) branching of Cu close to wing base (this part of the wing is not preserved in *B. occulta* but can be extrapolated from the course of the preserved parts of CuA+ and CuP–), (vi) branched CuA+ (probably plesiomorphic).

W. maryvonneae is quite similar to other hindwings in Protomeropidae. *B. occulta* however differs from all Protomeropidae in the following characters: (i) ScP– reaching anterior wing margin and probably distally not fused with RA+, (ii) CuA– not simple but with 3 terminal branches, and—probably the most important character—(iii) CuP– branched as rich as CuA+, the first branch (CuP_1–) extremely curved backwards. The first character is regarded as an apomorphy of the Protomeropidae by IVANOV & SUKATSHEVA (2002), whereas NEL et al. (2007) assume it to be a plesiomorphy at the level of Holometabola or even the whole Pterygota. Other plesiomorphic characters of *B. occulta* are the rich branching of ScP– (with 8 anterior branches) and RP– (with 9 terminal branches). The rich branching of CuP– and backward-curving especially of CuP_1– is quite unique in Late Carboniferous basal Neoptera.

Therefore it is concluded that *B. occulta* is vague related to the Protomeropidae but represents a separate new family of uncertain systematic placement. Both taxa might be stem group representatives of Endopterygota. In this case *B. occulta* would be the most ancient holometabolous insect.

(c) Prothoracic winglets – An alternative hypothesis for Baryshnyala occulta?

Lateral lobate prolongations are common in early Pterygota. They are considered either as prothoracic winglets (e.g. KUKALOVÁ-PECK 1991 and references therein) or secondary pronotal lobes (e.g. RASNITSYN &QUICKE 2002 and references therein).

Recently ILGER & BRAUCKMANN (2008) reported a first evidence of such structures in *Kochopteron hoffmannorum* and interpreted them as true winglets, i.e. a serial homology to meso- and metathorcic wings (see chapter 5.1.1). In this case prothoracic winglets are part of the groundplan pattern of all Pterygota (both “Palaeoptera” and Neoptera) and represent a strongly plesiomorphic character. The reduction of such winglets is secondary and a derived trait that was independently developed in higher Pterygota. For these phylogenetic reasons it is assumed that prothoracic winglets potentially existed in basal Neoptera and not only in *K. hoffmannorum*. In previous reconstructions (e.g. BRAUCKMANN & SCHÖLLMANN 2005: Fig. 27) such winglets are already indicated.

Their presence in *K. hoffmannorum* shows that prothoracic winglets in basal Neoptera might have been more wing-like than in certain "Palaeoptera" where their shape is rather lobate or semi-circular. Specimen WMf.N P.26093 pos. of *K. hoffmannorum* shows prothoracic winglets as well as meso- and metathoracic wings. Thus the length/width ratios of all three pairs of wings can be measured. It is supposed that similar proportions could be potentially present in other basal Neoptera. Measurements for specimen WMf.N P.26093 pos. are: (i) prothoracic winglets: length ≈ 6.5 mm, width ≈ 3.0 mm, (ii) mesothoracic wings: length ≈ 37,5 mm, width ≈ 13.5 mm, (iii) metathoracic wing: length ≈ 38.3 mm, width ≈ 12.1 mm. The prothoracic winglets in *K. hoffmannorum* are much smaller than the wing of *Baryshnyala occulta*. If the same proportions would be present in the larger *Kemperala hagenensis* the following estimated size can be postulated: length ≈ 7.9–12.7 mm, width ≈ 4.0–5.4 mm. This range fits very well to *B. occulta* (see Fig. 16 on p. 42).

But it can be excluded that *B. occulta* is a prothoracic winglet of *Kemperala hagenensis* because the venation pattern differs as follows: (i) clearly pectinate cross-veins in costal area in *B. occulta* versus a fine meshwork in *K. hagenensis*, (ii) ScP– most probably reaching costal margin in *B. occulta* versus fusing to RA+ in *K. hagenensis*, (iii) CuP– with 3 terminal branches (1–2 in *K. hagenensis*), and (iv) strongly terminal convexity in posterior MP–, CuA+ and CuP– in *B. occulta*, (v) archedictyon not present in *B. occulta* but a number of straight cross-veins, (vi) corrugation not as well expressed as in *K. hagenensis*.

6 Taphonomy of Hagen-Vorhalle

Investigations of the ~210 Neoptera specimens from Hagen-Vorhalle have shown that virtually all specimens bear tiny globules on their wing surfaces. This fact was already perceived in earlier studies (several personal communications), but has never been published or systematically investigated, since the focus was always on the insects or attached ecto-parasites (i.e. BRAUCKMANN et al. 2007). There have been only two passing mentions of these structures by ILGER & BRAUCKMANN (2009) and BRAUCKMANN et al. (2010), but without any detailed taphonomic model.

After visual inspection of all specimens from the locality it became clear that these globules cannot be found in any other taxon, especially not in the ~100 specimens of associated "Palaeoptera". More than 98% of the globules have diameters of ~0.8–1.2 mm and <2% of them reach ~1.3–1.4 mm at the maximum and have a rounded, triangular shape eccentrically enclosing the globule. Morphological analysis revealed that they are shells of young bivalves. Spherules are prodissoconchs (= shells of the veliger and veliconcha larval stage) and sub-triangular shells are the youngest dissoconchs (= shells of an early spat stage). Their surface is always smooth with a rolling suture between the prodissoconch and dissoconch (Fig. 17). Prodissoconchs are uniform and do not show any separation in a stage I and II (Fig. 18–19).

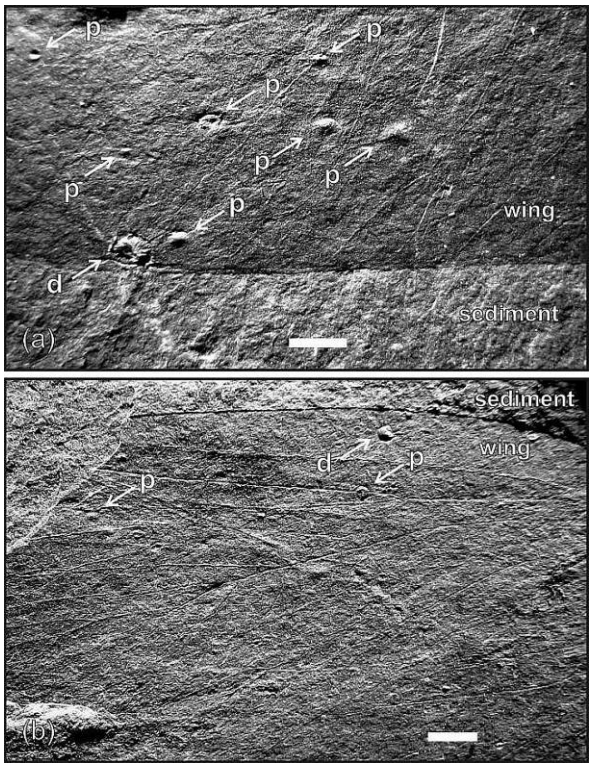


Fig. 17: Detail of Neoptera wings bearing prodissoconch (p) and dissoconch (d) of *Naiadites vorhallensis* Huwe, 2006. **(a)** *Kemperala hagenensis* BRAUCKMANN, 1984 (specimen WMf.N P.20546), posterior margin of mesothoracic wing. **(b)** *Holasicia rasnitsyni* BRAUCKMANN, 1984 (specimen WMf.N P.27840 neg.), overlapping meso- and metathoracic wings. Scale bars: 2 mm.

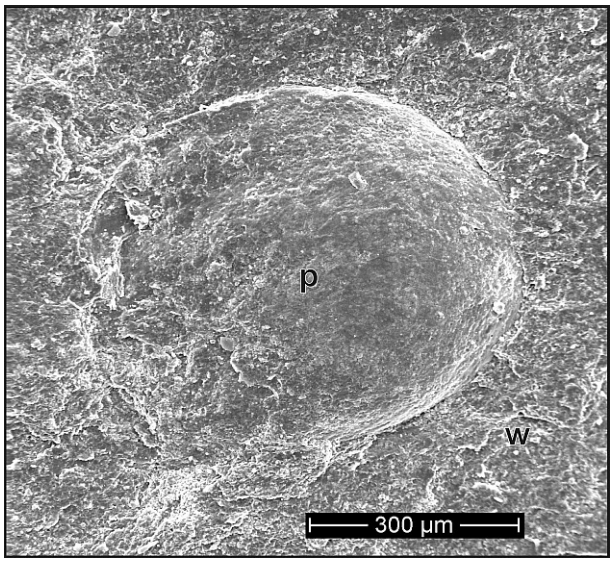


Fig. 18: SEM image of a prodissoconch of *Naiadites vorhallensis* HUWE, 2006 showing bivalve shell (p) surrounded by insect wing membrane (w) of Neoptera inc. sed. (specimen WMf.N P.22616 [H64]).

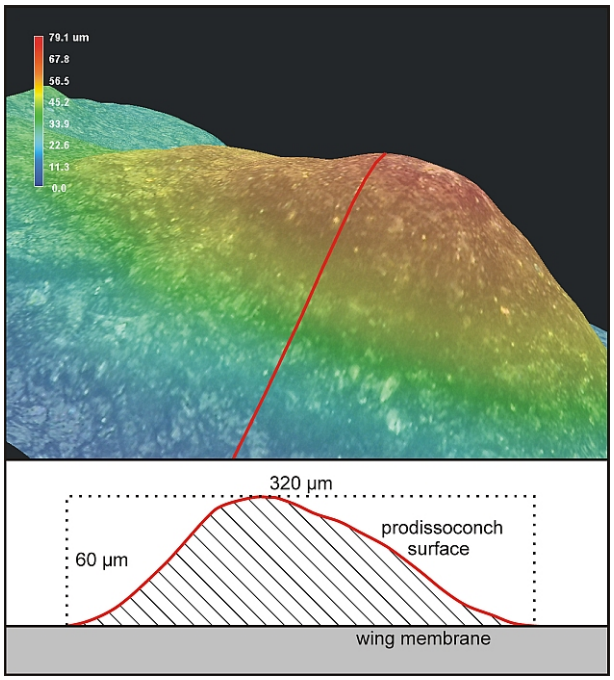


Fig. 19: Three-dimensional microscopy scan of a prodissoconch of *Naiadites vorhallensis* HUWE, 2006. Red line indicates profile line across prodissoconch surface. Note the smooth surface of the bivalve shell lacking a prodissoconch II stage.

In some cases the shells are detached during recovery and preparation of the insect wings. In these cases a remaining negative indentation traces their form and shape. Embedding is always dorso–lateral, such that the sagittal plane of the shells is parallel to the insect wing membrane. Due to preparation of the wings, either the left or right valve is visible. No byssi or other fibers

attaching to the wings are visible, either due to preservation or perhaps destruction during decay or diagenesis. However it can be assumed that the shells are in their in-situ, life position.

The bivalve fauna of Hagen-Vorhalle has been described in detail through the fundamental work of HUWE (2006) (see chapter 2.3). According to her work, and personal communication, prodissoconchs can be assigned to *Naiadites vorhallensis* HUWE, 2006 (Pteriomorphia BEURLEN, 1944: Pterioida NEWELL, 1965: Myalinidae FRECH, 1891); a species well known from this locality through all ontogenetic stages. The observed shells fit very well in size, shape and structure (Fig. 20). In any case an unequivocal determination is very difficult due to the early ontogenetic stages of the individuals which show few diagnostic characters and which can be similar in different taxa.

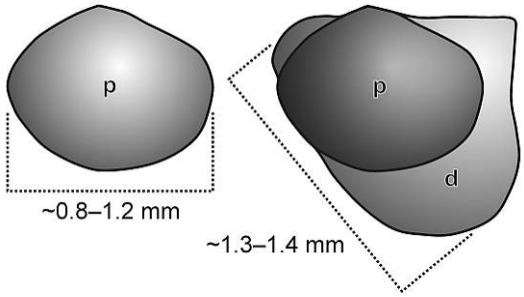


Fig. 20 Schematic drawing of a prodissoconch (p) and dissoconch (d) stages of *Naiadites vorhallensis* Huwe, 2006 with general measurements. Modified after Huwe (2006).

A systematic inspection of the material showed that the shells do not occur in the close-by sediment but only on the wing itself. In only a few specimens isolated shells are obviously disrupted from the wings and embedded close to the wing margin. Furthermore they cannot be found on other surfaces of the insect bodies such as the head, antennae, thorax, legs or tarsi, even though these are also well preserved. So far they were not found on prothoracic winglets in Neoptera (ILGER & BRAUCKMANN 2008), but this may be due to preservation.

Detailed observation has shown that the shells are limited to the dorsal sides of the wing membranes. Mesothoracic wings usually overlap the metathoracic ones in a typical V-shaped resting position (one of the key characters for assigning the taxa to Neoptera, see e.g. BRAUCKMANN et al. 2010). Thus some specimens exhibit bulges in the forewings that result from shells on the underlying hindwing that are not attached to the forewing's ventral side.

Virtually no Neoptera-wing is without bivalves, even though they are sometime barely visible and disguised by tectonic schistosity (see chapter 2.5 for tectonics).

The best preserved wings show up to >50 individuals on one single wing. That means a density of ~12.5 cm^{-2}. A difference between the three Paoliidae species cannot be recognized, but wings of *Heterologopsis ruhrensis* (family ?Carcurgidae) seem to bear less shells per unit area. This

may be caused either by differences in the wing membrane structure or by the much smaller size of the species.

The main argument for an in-situ position of the bivalve shells is that they are limited to the wing surfaces and are absent from the surrounding sediment. They are also lacking in the over- and underlying laminae, so their embedding must have been synchronous to the embedding of the insects.

This could be explained by a contemporaneous death of the insects and bivalves, for instance by a local mortal event (e.g. water/air intoxication, dramatically changing weather, etc.). But in this case insects and bivalves would originate from a kind of undifferentiated dropping from the upper water body, and would be found all-over on distinct strata. Furthermore this approach cannot explain why only Neoptera should have been affected, but no "Palaeoptera" specimens. Moreover it is assumed that the insects did not live directly in the delta complex, but in swamps and bayous in the forelands and were transported in the delta either by short fluvial or aerial transport.

The same arguments contradict the assumption that there was a continuous or periodic dropping of young bivalves as per reproductive seasons or changing water currents.

As the shells are limited to the wings and do not occur on other parts of the insect body it can be concluded that they really were attached to the wing membranes as their living habitat. Free-swimming planktonic trochophore larvae (developing from a blastula) and veliger pick an adequate habitat to settle for the rest of their life cycle. In *Naiadites vorhallensis* this is typically a drifting piece of wood (HUWE 2006). This has the load-bearing capacity and buoyancy to float with a colony of adult bivalves for a long time. As this settlement is not an active selection process the bivalves cannot differentiate between wings and wood. Key parameters might be orientation, exposition, surface properties and simple availability of a potential substrate.

The fact that the shells are limited to the dorsal surface of the wings is of great interest for reconstructing the taphonomy. The larval stages must have been continuously covered with water. They soon die when they become dry. Adult bivalves may endure short periods of relatively dryness (e.g. specimens from tidelands) but these young larval stages have not the same capability of preventing evaporation from their tissue by enclosing. On the other hand the anatomy of the insects with their remarkably long and slender legs and antennae would have prevented drifting upside-down. The body will always turn back to a position with hanging extremities and appendages. Thus the only possibility is that the insect body did not drift along the water/air contact, but became submerged somewhere within the water body.

Detailed SEM images show that the prodissoconchs are always uniform and do not have a suture line separating the prodissoconch I and II stage. This is a character which has implications for the larval feeding behavior. As Ó FOIGHIL & GRAF (2000) stated in an example using the ontogeny of Recent *Neotrigonia margaritacea* (LAMARCK, 1804) (Pteriomorphia: Trigonioida DALL, 1889: Trigoniidae LAMARCK, 1819) the lack of a PII stage usually contradicts planktotrophy.

N. vorhallensis is allocated to the Myalinidae which are primary planktotrophic. But it is likely that taxa from fresh and brackish water became secondary yolk-feeders (= lecithotrophy). Life in an aquatic habitat of reduced salinity is further supported by HUWE (2006).

The fact that bivalve shells occur exclusively on the dorsal side of the wings indicates that this side was exposed to appropriate living conditions, whereas conditions on the ventral side were hostile.

Once *Naiadites* larvae have settled on a substrate they will become sessile for the rest of their lives. Not more than ~2% of all bivalves attached to insect wings had reached the early stage of a spar developing a dissoconch. This may indicate that the habitat conditions changed at this stage of ontogeny, and that larval development ended with the death of the bivalves. The most plausible reason is obviously the embedding of insects and attached shells into the sediment on the seafloor. Presumably this was associated with the increasing weight of the wing caused by growing shells that resulted in an overall decrease in buoyancy.

The time span between attachment of the free-swimming larvae to the wings and their death gives a sense of the drifting period. On the other hand it is very hard to assess how fast the ontogenetic rate was in fossil bivalves. Comparison with Recent Bivalvia can only be a limited approximation. An example from the development of *Pandora inaequivalvis* (LINNAEUS, 1758) (Anomalodesmata DALL, 1889: Pholadomyoida NEWELL, 1965: Pandoridae RAFINESQUE, 1815) given by ALLEN (1961) shows that the time span of prodissoconch growth is about 3–4 days subsequently followed by the growth of the dissoconch. The growth rate of the larval shell is highest in the early prodissoconch stage. These rates are not only a function of the taxon, but are also influenced by temperature, nutrition and water chemistry. Nevertheless a period of some days, up to one week, is likely for the *N. vorhallensis* specimens on wings.

Microbial mats: An alternative hypothesis?

Micro-organisms are widely common and probably omnipresent in aquatic habitats. They can build up mats of complex communities on the surfaces of drifting objects (both organic and inorganic). Such microbial mats consist of photosynthetic prokaryotes, diverse unicellular "algae," and chemo-autotrophic micro-organisms (GALL, 1990). Anaerobic and aerobic species can coexist in one habitat. The growth and biological activity of these micro-organisms may facilitate the preservation of insects in a number of ways as presented by BRIGGS (2003).

Micro-organisms, such as Cyanobacteria and others, may be spherical or filament-like and form a mat by secreting mucilage. It can be presumed that such an agglomeration would be visible in the extraordinarily well preserved material from Hagen-Vorhalle. Investigations of the entire Pterygota material (insect wings, their margins, and attached bivalves) under normal, polarized, and ultraviolet light at high magnifications, with a SEM and EDX unit, and a digital

2D/3D microscope did not find proof of any such structures. In no case was any kind of microbial-like configuration found.

Furthermore, it can be assumed that a dense colonization with microbial mats would have suppressive effects on bivalve attachment and growth. Both types of organisms would have competed for habitat and biotope. Such a dense colonization (Fig. 21) of the wings by prodissoconchs and even dissoconchs can hardly be explained with coexisting dense microbial mats. It is supposed that micro-organisms existed but were not dominant during taphonomic processes in Hagen-Vorhalle. Most probably real "mats" did not occur. Potentially insect corpses were affected by (?anaerobic) micro-organisms that facilitated the preservation when reaching the bottom. Certainly this cannot be proven beyond doubt, but it might be a potential explanation for the extraordinarily well-preserved material of the Lagerstätte in general.

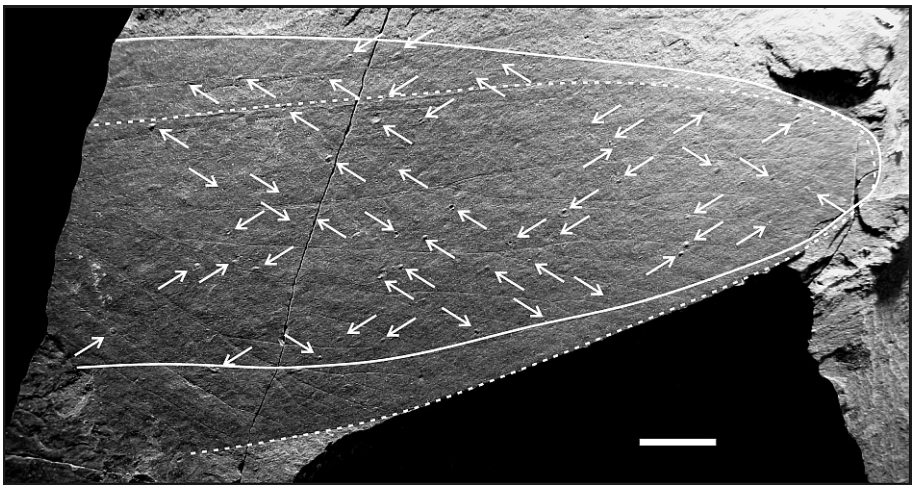


Fig. 21: Overview photograph of two overlapping wings of Neoptera (*Kemperala hagenensis* BRAUCKMANN, 1984; specimen WMf.N P.27823 neg.). Continuous line surrounds mesothoracic wing, dashed line indicates metathoracic wing. Arrows pointing at >50 attached bivalve shells of *Naiadites vorhallensis* Huwe, 2006 on the forewing. That means a "bivalve density" of ~12.5 cm^{-3}. Scale bar: 5 mm.

Taphonomic model

Based on the results and parameters above, the most plausible taphonomic scenario involves a drifting insect corpse within an open body of water. Due to high surface freshwater inflow and very low tidal ranges the water column was strongly stratified. During the drifting period insects wings were infected by free-swimming bivalve larvae that derived from the fluvial freshwater and were washed into the brackish milieu of the deltaic complex.

With respect to the observed preservation pattern, ontogenetic age and size of the young bivalves, and their exclusive occurrence on dorsal wing membranes, a taphonomic scenario with six stages (Fig. 22) can be reconstructed:

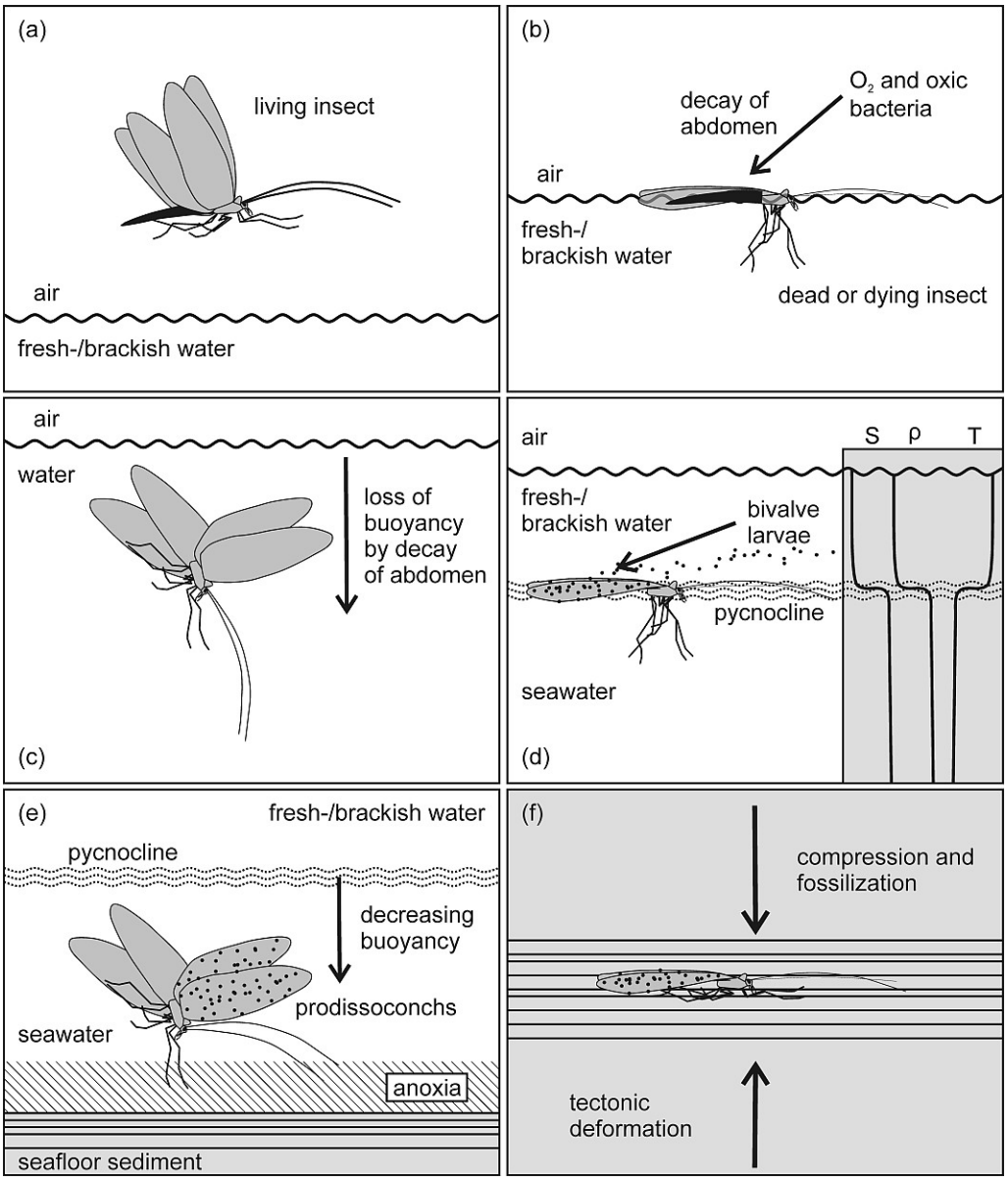


Fig. 22: Taphonomic model of Hagen-Vorhalle. **(a)** Living Neoptera insect. **(b)** Drifting of the dead or dying insect corpse at the air/water contact layer. Soft-tissued abdomen begins to decay first. **(c)** After loss of the abdomen by decay, buoyancy decreases and corpse begins to sink. **(d)** Insect reaches the pycnocline of the strongly stratified water body. During intra-water column drifting the dorsal sides of the wings are infected by free-swimming bivalve larvae. Schematic graphs on the right show trends of salinity (S), density (ρ) and temperature (T). **(e)** Insect corpse breaks through pycnocline when weight of prodissoconchs increases and reaches anoxia near the seafloor. **(f)** Embedding in sediment and beginnings of diagenesis and fossilization.

Description of the six stages of the model

1. Both “Palaeoptera” and Neoptera lived in the coastal forests and swamps near Variscan forelands. They lived in a widespread area during the Marsdenian and maybe early Yeadonian. Sometimes living insects, or their corpses, fell into the river or directly into the deltaic complex. A short eolian transport by wind or storms is also possible. The

body, dead or dying, drifts along the water/air interface. Under oxic conditions it was affected by decay processes.

2. At this early stage of the model there is a major difference in the decay behavior of "Palaeoptera" and Neoptera. The first had a harder, better sclerotizied abdomen with very long cerci such that their drifting period on the water surface might not have been very long. Afterwards they sank directly to the seafloor and were embedded in the sediment. Due to this short period between death and embedding, decay could only briefly occur, leading to very well preserved fossils. – On the other hand Neoptera had a soft-tissued abdomen that began to decay immediately after death. This process was probably influenced by oxic bacteria. Differences in drifting and sinking behavior in "Palaeoptera" and Neoptera can probably be explained by their different abdomen. The soft abdomen of the latter may have served as a kind of "swimming buoy". Buoyancy might have been benefited by an inflation of fermentation gases. A number of taphonomic experiments and considerations by different authors (e.g. WILSON 1988; MARTÍNEZ-DELCLÒS & MARTINELL 1993; MARTÍNEZ-DELCLÒS et al. 2004; MARTÍNEZ-DELCLÒS & NEL 2000; LUTZ & KAULFUß 2006) have shown that even heavier sclerotizied insects can be influenced by a strongly stratified water column. However, the attachment of young bivalves to a distinct group of insects and their lacking in other groups cannot be explained by these models.
3. After the abdomen was (completely or at least partly) decayed the buoyancy of the remaining body decreased. Thus after a short drifting period the remaining corpse begins to sink.
4. Within a strongly stratified water column the corpse could temporarily stop sinking at a pycnocline caused by a vertical density gradient. The denser seawater underlay the lower density fresh-/brackish water. Perhaps temperature (seawater: relatively cooler; fresh-/brackish water: warmer) also played a role here? A second period of drifting along the pycnocline began. During this stage the dorsal wing surface was exposed to the fresh-/brackish water and the ventral side to the seawater. This drifting position was very stable due to the long, sagging legs and antennae. – Free-swimming, lecithotrophic (= feeding on a yolk) bivalve larvae became introduced from the river into the deltaic system. They encountered an ideal habitat for settling on drifting insect wings. As the larvae were restricted to brackish water they did not settle on the ventral sides.
5. Attached to the wings, bivalve larvae entered their early sessile stage by developing a globular prodissoconch. After a certain time (possibly some days, up to a week) they reached diameters up to ~1.2 mm. A few specimens even reached the next stage and built up a rounded triangular dissoconch with diameters up to ~1.4 mm. – At this time, obviously triggered or at least aided by the increasing weight of the growing bivalves, the insect/bivalve association broke through the pycnocline due to loss of buoyancy.

6. Once in the seawater strata, the bivalves quickly died due to high salinity of the tropical seawater. Finally the insect body, with attached shells, reached the seafloor and was embedded in the sediment. A near-seafloor anoxia might have led to the extraordinary preservation of the remaining body structures and stopped any further decay. When diagenetic processes and fossilization began the bivalves were already fixed at the ontogenetic stage they had reached when penetrating the pycnocline.

7 Exploration of new Lagerstätten – Küchenberg locality near Fröndenberg

7.1 Location and overview

Until the discovery of the Konservat-Lagerstätte of Hagen-Vorhalle and the Qilianshan (Ningxia) region in northern China (e.g. PENG et al. 2004; PROKOP & REN 2007), Namurian (Late Carboniferous, Pennsylvanian) insects were generally extremely rare, and most of the few then known localities yielded only one single or two remains.

Fossiliferous rocks that are nearly contemporaneous to those from Hagen-Vorhalle are also accessible in two different sites near Fröndenberg/Ruhr, ~25 km NE Hagen-Vorhalle (JENCHEN & SCHULTKA 1993), i.e. the former brickyard quarry Voßacker and an abandoned quarry at the Küchenberg between Fröndenberg and Ardey (Fig. 23). Most of the recent collections in this area have been gathered by H. Bech and G. Sommer (see chapter 3.3.2). Both sites mainly yielded fossil plants as did Hagen-Vorhalle. Additionally, a typical Namurian marine fauna was reported by JENCHEN & SCHULTKA (1993) from the Voßacker section, including Brachiopoda, Bivalvia, orthocone Cephalopoda, and "fish" s.l. remains. In assition, a single isolated wing of *Kemperala hagenensis* was mentioned by the authors (JENCHEN & SCHULTKA 1993: 46).

Among animal remains, only a few "fish" scales and a single specimen of *Bellinurus* cf. *truemani* DIX & PRINGLE, 1929 (Merostomata WOODWARD, 1866: Xiphosurida SNODGRASS, 1938) have been reported (JENCHEN & SCHULTKA 1993; SCHULTKA 1994). Additionally, some trace fossils of *Sinusites* type (sensu SEILACHER 1963: 82–83) occur.

In the present thesis the first insect remains, belonging to three different species, are described from the Küchenberg section. Two of them, *Homaloneura berenice* and *Kochopteron hoffmannorum* have already been reported from Hagen-Vorhalle; the third species, *Bechala sommeri*, is newly introduced.

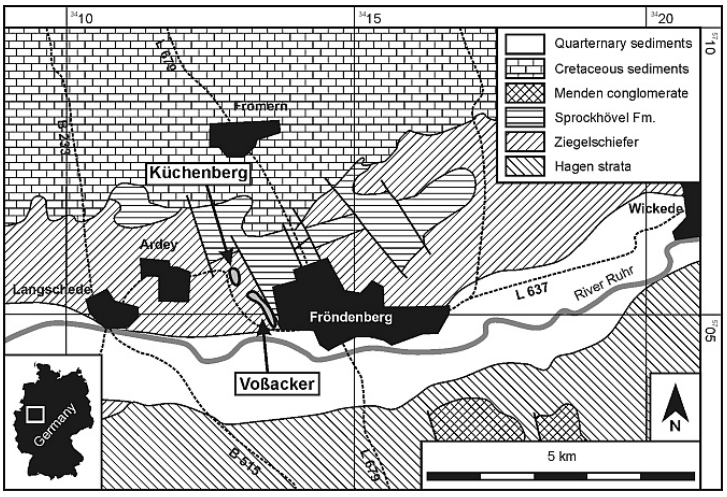


Fig. 23: Geological map of the Fröndenberg area. The abandoned Küchenberg and Voßacker quarries are indicated. Modified after SCHULTKA (1995).

With the Küchenberg section a new locality in the southern Ruhr area is known, the stratigraphical age of which is believed to be nearly contemporaneous with Hagen-Vorhalle or only slightly younger.

The Küchenberg is a hill between the town of Fröndenberg and the village of Ardey in the Unna district, North-Rhine Westphalia, western Germany. The abandoned quarry is located close to the southern brookside of the Osterholzbach at its northwestern slope at approx. N 51° 28.48', E 007° 44.26'; ~160 m a.s.l. The section is about 67 m long, and the area of former mining is located at the eastern face which is nearly 25 m high. The site lies ~650 m NW of the former Voßacker quarry, which was described in detail by JENCHEN & SCHULTKA (1993), and from where a single wing of *K. hagenensis* is known. The whole area is covered by the geological map of North Rhine-Westphalia 1:25,000, sheet no. 4512 Menden.

7.2 Stratigraphy, facies, and taphonomy

Since the fossil record from the Küchenberg site lacks marine taxa (vide infra) the biostratigraphical allocation is based upon certain plants. These are Calamitales (e.g. *Mesocalamites haueri*, *Asterophyllites* sp., *Annularia jongmansi*) and pteridophylls (e.g. *Eusphenopteris hollandica*, *Mariopteris acuta*, *Neuralethopteris schlehani*, *Paripteris gigantean*, and other species (see JENCHEN & SCHULTKA 1993 for further information and references). Most of the plant remains are unusually tiny leaves and litter. Currently the Küchenberg flora is under investigation by S. Schultka (Museum für Naturkunde Berlin; Germany), which may lead to a specification of the age. He also reports (personal communication 2010) that there are abandoned sinks and fault pits close to the outcrop which indicate the occurrence of coal seams. They may belong to Flöz Sengsbänksgen or Flöz Sengsbank of the local terminology. These are the oldest coal seams in the Ruhr area (Sprockhövel-Schichten; formerly "Magerkohle"). Thus the strata are slightly younger than those in the former brickyard quarry Voßacker at Fröndenberg (e.g. SCHULTKA 1995). They may be of latest Namurian B age (Marsdenian: ammonoid zone R2: higher Ziegelschiefer Formation or Kaisberg Formation, early Bashkirian). Even an early Namurian C age cannot be excluded (Yeadonian: ammonoid zone G1: Sprockhövel Formation).

Since the Late Carboniferous stratigraphy is largely based on marine index fossils (e.g. ammonoids) the exact dating of the mainly limnic/terrestrial Küchenberg strata is problematical. For a detailed description of the entire section see JENCHEN & SCHULTKA (1993: 54–55).

Not all of the samples taken by private collectors are stratigraphically referenced. It is therefore difficult to allocate the specimens to distinct strata. Referring to facies and lithology, the insects might originate from the same sediment package as the xiphosurid and the trace fossils (vide infra). For a lithological overview see Figure 24.

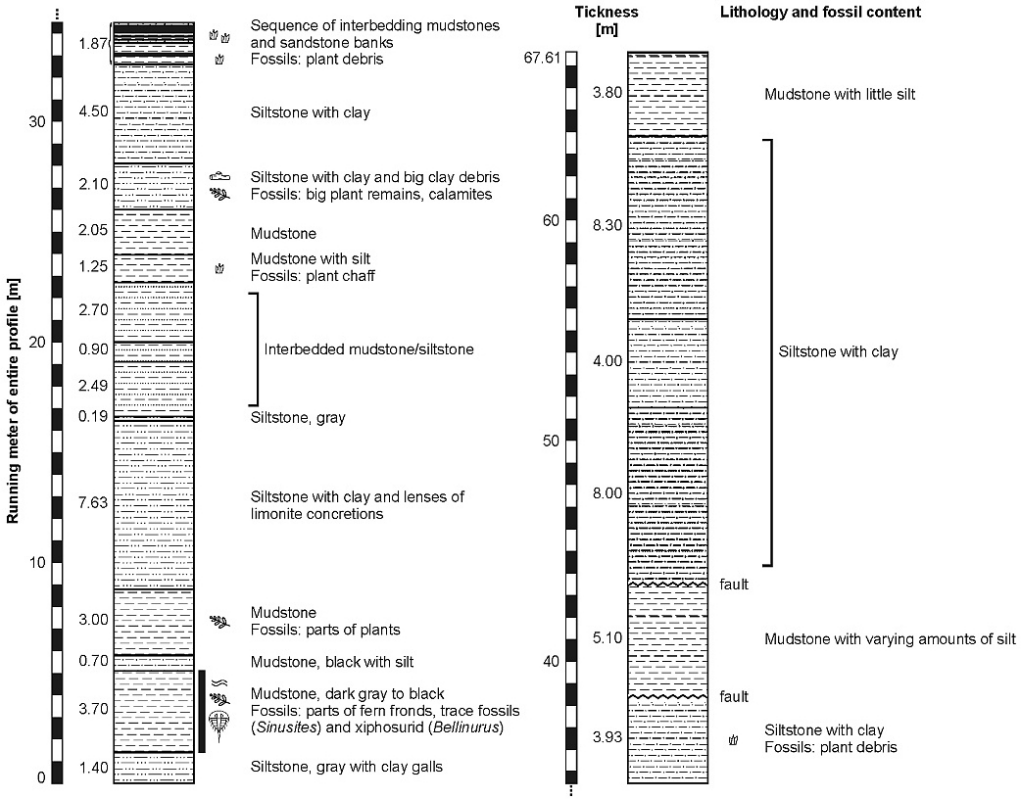


Fig. 24: Section of the Küchenberg quarry (data and measurements modified after information in JENCHEN & SCHULTKA 1993: 54–55). Vertical black bar on the left profile indicates most probable position of insect bearing strata.

Whereas both Hagen-Vorhalle and Voßacker represent deltaic facies (see chapters 2.6 and 6), the Küchenberg section does not show any marine influence (JENCHEN & SCHULTKA 1993). The occurrence of the xiphosurid *Bellinurus* cf. *truemani* and trace fossils of *Sinusites* type indicate a non-marine period. SCHULTKA (1988) assumes a widespread freshwater area which was dammed up by marine transgressions in the hinterland. Most plant remains from both Voßacker and Küchenberg are seriously fragmented. This indicates a long transport with high water energy. A major river draining the Variscan Orogen in the south seems to be a possible transport medium. The insects wings reported in this paper are also isolated and fragmentary. In none of the specimens was the wing base and articulation preserved. Contrary to Hagen-Vorhalle where nearly complete preserved Pterygota occur, we suppose that the Küchenberg specimens were transported over a longer distance. Since the swamps and bayous were closely adjacent to the Hagen-Vorhalle delta, they might have been more upstream in Küchenberg. Thus an eolian transport of the airy wing fragments is also possible.

7.3 Systematic paleontology of Küchenberg

Order Palaeodictyoptera GOLDENBERG, 1877

Family Spilapteridae HANDLIRSCH, 1906

Genus *Homaloneura* BRONGNIART, 1885

Type species: *Homaloneura elegans* BRONGNIART, 1885 (Stephanian B; Commentry, France).

Other Namurian species included in *Homaloneura*: *H. ligeia* (late Namurian B; Hagen-Vorhalle, Germany), *H. berenice* (late Namurian B; Hagen-Vorhalle, Germany). The whole genus includes about 11 species which cover a stratigraphical range from Namurian B (Marsdenian) to Stephanian in Europe (France, Germany, Portugal) and North America (USA) (see BRAUCKMANN et al. 2003).

***Homaloneura berenice* BRAUCKMANN & GRÖNING 1998**
Fig. 25a–b, 26a–h; Tab. 1–3

v* 1998 *Homaloneura berenice* BRAUCKMANN & GRÖNING: 77–84, figs. 1a–3c.
v 2003 *Homaloneura berenice*.– BRAUCKMANN et al.: 15–17, figs. 2–3b, pls. 1–2.

Holotype: Specimen no. WMf.N P.30360B; Namurian B (Marsdenian); Hagen-Vorhalle. BRAUCKMANN & GRÖNING (1998: 80) still used its preliminary number ("K-12") of the M. Kemper collection.

Additional material from Hagen-Vorhalle: specimen no. WMf.N P.20629, nearly complete, head and distal part of abdomen lacking; specimen no. WMf.N P.15180, complete pairs of mesothoracic and metathoracic wings; both of them deposited in the collection of the LWL-Museum für Naturkunde in Münster.

New material from the Küchenberg site: Seven specimens: AKH 294 a (negative print) and b (positive print) – isolated right metathoracic wing; AKH 540 a (positive print) and b (negative print) – disrupted distal third of a right metathoracic wing; AKH 542 a (positive print) and b (negative print) – disrupted distal three-fourths of a right mesothoracic wing; AKH 1517A a (positive print) and b (negative print) – isolated right metathoracic wing; AKH 1517B a (positive print) and b (negative print) – disrupted distal three-fourths of a right mesothoracic wing; AKH

1515 a (positive print) and b (negative print) – disrupted half of a left mesothoracic wing; AKH 1514 a (positive print) and b (negative print) – small disrupted apical area of a left (?mesothoracic) wing.

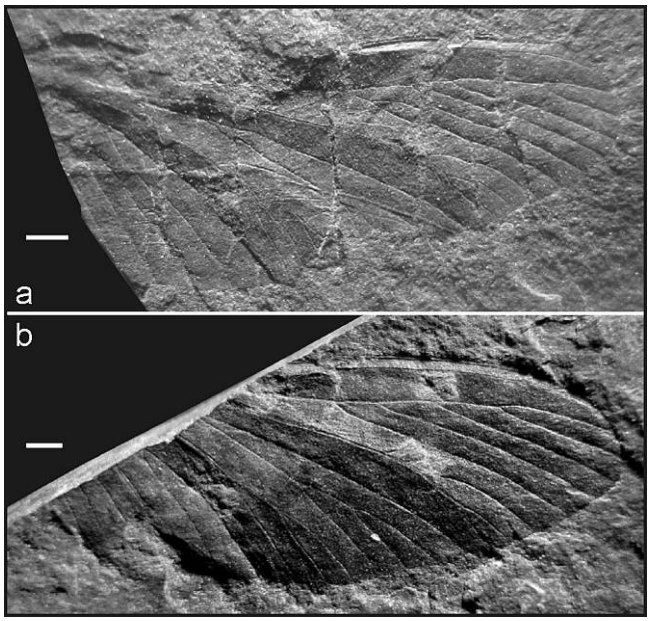


Fig. 25: *Homaloneura berenice* BRAUCKMANN & GRÖNING, 2003 (Spilapteridae HANDLIRSCH, 1906) late Namurian, Küchenberg quarry, positive prints of two of the seven specimens. Both specimens show the distinct corrugation and some of the colored spots under polarized light. For interpretation and vein nomenclature see Fig. 4. **(a)** Specimen AKH 1517A a, isolated right metathoracic wing. **(b)** Specimen AKH 542 a, distal three-fourths of a right mesothoracic wing. Scale bars: 1 mm.

Diagnosis: See BRAUCKMANN & GRÖNING (1998); BRAUCKMANN et al. (2003). The new material does not provide completely new characters that are significant for diagnosis but serves to broaden the knowledge of intra-specific variability both in venation pattern and size (vide infra).

Measurements (see also Table 1 and discussion below):

Mesothoracic wing: length (extrapolated): ~14.0–17.0 mm, width: ~5.2–6.3 mm; metathoracic wing: length (extrapolated): ~13.5–15.2 mm, width: ~5.0–5.5 mm.

Preservation: All specimens from the Küchenberg site are isolated wings or wing fragments without any additional structures of the body, wing base or articulation. Five of the seven wings are well preserved but in each of them the basal part and the proximal anal area are lacking. Thus the complex AA+/AP– is poorly preserved. One specimen (AKH 1514) is a disrupted apical area showing all terminal branches of RA+ and RP– as well as the most anterior branch of MA+. In all wings the corrugation is quite visible although it seems to be flattened by diagenesis and tectonics. In general, the tectonic deformation rate seems to be low. Three wings (AKH 542; AKH 1515; AKH 1517A) show remains of a color pattern which is visible in acute-angled view

under polarized light. One wing (AKH 294) is disrupted and kinked in sub-longitudinal direction (from mid-anterior margin to posterior margin between RP– and MA+), covering the course of the anterior branches of MA+.

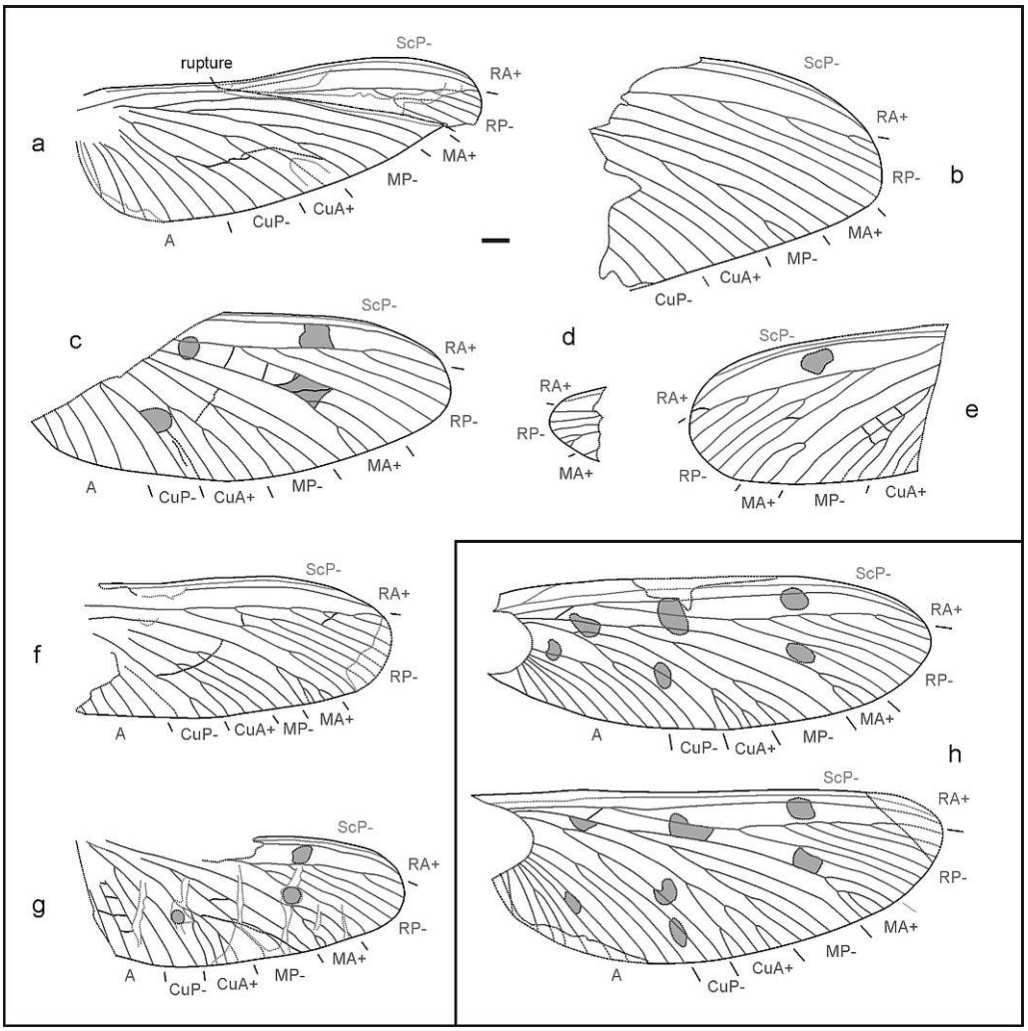


Fig. 26: *Homaloneura berenice* BRAUCKMANN & GRÖNING, 2003 (Spilapteridae HANDLIRSCH, 1906) late Namurian, Küchenberg quarry, synopsis of interpretative drawings of the venation and color patterns. **(a)–(g)** The seven wings from the Küchenberg quarry. The images were produced considering both the positive and negative prints in combination. **(a)** AKH 294 a/b: isolated right metathoracic wing. **(b)** AKH 540 a/b: distal third of right metathoracic wing. **(c)** AKH 542 a/ b: distal three-fourths of right mesothoracic wing. **(d)** AKH 1514 a/b: small apical area of left (?mesothoracic) wing. **(e)** AKH 1515 a/b: distal half of left mesothoracic wing. **(f)** AKH 1517B a/b: distal three-fourths of right mesothoracic wing. **(g)** AKH 1517A a/b: isolated right metathoracic wing. **(h)** Holotype (WMf.N P.30360B), almost completely preserved forewing and hindwing, Namurian B, Hagen-Vorhalle, for comparison. Scale bar for a–h: 1 mm

Remarks: The differentiation of mesothoracic and metathoracic wings is very difficult in isolated wings since they are nearly homonomous. It depends mainly on three characters: (i) geometry of apex: in the metathoracic wings the apex is slightly shifted in posterior direction; (ii) costal margin: nearly straight in mesothoracic wings, but more concave at mid-wing part of metathoracic wings; (iii) anal area: slightly broader (but never lobate) in metathoracic wings. Since only isolated wing fragments are known from the Küchenberg it cannot be decided if

there might be a certain kind of sexual dimorphism expressed in the wing geometry as reported by Beckemeyer and Byers (2001) for the Early Permian Spilapteridae HANDLIRSCH, 1906b species *Dunbaria fasciipennis* TILLYARD, 1924 from Kansas (USA).

Tab. 1: Measurements of forewings and hindwings in *Homaloneura berenice* BRAUCKMANN & GRÖNING, 2003. FW: forewing; HW: hindwing; l: length [mm]; w: width [mm]; l/w: ratio length/width [-]. For better comparison data of *H. ligeia* Brauckmann, 1986 from Hagen-Vorhalle are also stated. Annotations: [1] Data from BRAUCKMANN (1986: 60–63), [2] Data from BRAUCKMANN & GRÖNING (1998: 80–82).

Specimen	FWl	FWw	FWl/w	HWl	HWw	HWl/w
H. ligeia						
Holotype[1]	~30.8	~12.7	2.4	~30.3	~14.5	2.1
H. berenice						
Holotype[2]	17	6	2.8	17	6.6	2.6
AKH 542	~17	~6.3	2.7	-	-	-
AKH 1517B	~14.2	~5.2	2.7	-	-	-
AKH 294	-	-	-	~16	~5.5	2.9
AKH 1517A	-	-	-	~14.5	~5.1	2.8

Tab. 2: Venation pattern in *Homaloneura berenice* BRAUCKMANN & GRÖNING, 2003: Number of terminal main vein branches in forewings. For better comparison data of *H. ligeia* BRAUCKMANN, 1986 from Hagen-Vorhalle are also stated. Annotations: * Variability of left and right forewing, [1] Data from BRAUCKMANN (1986: 60–63), [2] Data from BRAUCKMANN & GRÖNING (1998: 80–82), [3] Data from BRAUCKMANN et al. (2003: 15–17).

Specimen	RP-	MA+	MP-	CuA+	CuP-
H. ligeia					
Holotype[1]	8	6–7*	3–4*	5–6*	3
H. berenice					
Holotype[2]	7	3	4	3–4*	3
"2nd specimen"[3]	6	3	4–5*	4	(?1–)3*
AKH 542	5	3	4	3	2
AKH 1514	6	-	-	-	-
AKH 1515	6	2	4	3	-
AKH 1517B	9	5	2	3	?3

Tab. 3: Venation pattern in *Homaloneura berenice* BRAUCKMANN & GRÖNING, 2003: Number of terminal main vein branches in hindwings. For better comparison data of *H. ligeia* BRAUCKMANN, 1986 from Hagen-Vorhalle are also stated. Annotations: * Variability of left and right hindwing, [1] Data from BRAUCKMANN (1986: 60–63), [2] Data from BRAUCKMANN & GRÖNING (1998: 80–82), [3] Data from BRAUCKMANN et al. (2003: 17).

Specimen	RP-	MA+	MP-	CuA+	CuP-
H. ligeia					
Holtype[1]	7–9*	5–6*	5	5	3
H. berenice					
Holotype[2]	7	4	4	5	2
"2nd specimen"[3]	7	(?1–)4*	4–5*	4	2
AKH 294	6	-	4	2(–?3)	3
AKH 540	5	3	4	3	3
AKH 1517A	6	4	3	4	2

Discussion

In size, shape, venation and color pattern the Küchenberg specimens closely resemble *Homaloneura berenice* from Hagen-Vorhalle: (i) Size: Because all wings are disrupted at their base the exact length cannot be measured. However the wing geometry permits us to extrapolate the original size (Tab. 1). It is very similar to the holotype in specimens AKH 542 and AKH 294. AKH 1517B and AKH 1517A are remarkably smaller, but this degree can be explained by tectonic shortening. As in the case of Hagen-Vorhalle the rocks are strongly stressed by tectonics (e.g. DROZDZEWSKI et al. 1996). (ii) The shape of mesothoracic and metathoracic wings resemble well those of the holotype. (iii) The general pattern of the main veins is as in the holotype but varies in details, i.e. in the number of terminal branches (see Tab. 2–3). This degree of intra-specific variation is well known from Carboniferous Palaeodictyoptera (see e.g. BRAUCKMANN 1991 for *Homoioptera vorhallensis* of the family Homoiopteridae) as well as from other groups (CUI et al. 2010 for *Sinonamuropteris ningxiaensis* PENG et al., 2005; Grylloblattodea BRUES & MELANDER, 1915). The highest degree of aberration in mesothoracic wing venation is present in AKH 1517B with 9 terminal braches of RP– (others 5–7), 5 in MA+ (others 2–3) and only 2 in MP– (others 4–5). (iv) Color pattern: In three Küchenberg wings (AKH 542; AKH 1515; AKH 1517A) non-fused spots in two transversal rows are visible. Those of the distal row are located in the interradial area shortly after forking of RP– and between RP– and MA+ slightly before or at terminal branching of MA+. Spots of the more mid-wing row are located between RP– and MA+ at mid-wing and between CuA+ and CuP– slightly before mid-wing. In the holotype the spots are very similarly distributed, but with an additional third row proximally. This area of the wing is not preserved in any of the Küchenberg specimens, but it can be assumed that this third row was present in those complete wings, too.

Order: Megasecoptera HANDLIRSCH, 1906

Remarks: Despite their similar venation, the Megasecoptera have been mainly separated from the Diaphanopterodea by differences in the wing articulation (KUKALOVÁ-PECK 1991): The latter could flex their wings back over the abdomen whereas the Megasecoptera were unable to do so. More recently, several authors (e.g. SINITSHENKOVA 1993; 2002; BÉTHOUX & NEL 2003; PROKOP & REN 2007; BÉTHOUX 2008) independently, and with different arguments, presented new conceptions for both groups or at least for parts of them which differ from earlier ones. In this thesis the authors follows KUKALOVÁ-PECK (1991). Since the Bechalidae show several characters which were believed to be typical for the Megasecoptera, we conventionally place them here in this order.

Compared with other Pterygota, the Megasecoptera are still rare in Namurian deposits worldwide and usually represented by isolated wings, except for the two nearly completely preserved specimens of *Brodioptera stricklani* NELSON & TIDWELL, 1987 (Brodiopteridae CARPENTER, 1963; earliest Namurian, Kinderscoutian; Utah, USA) and *Xenoptera riojaensis* PINTO, 1986 (Xenopteridae RIEK, 1955; probably late Namurian or early Westphalian; Malanzán, La Rioja, Argentina). *B. stricklani* is the most ancient species of the Megasecoptera. The Hagen-Vorhalle quarry has yielded two species, both represented by isolated wings: *Sylvohymen peckae* and *S. pintoi*. A higher number of Megasecoptera is still to be expected from the Chinese Xiaheyan entomofauna (Namurian; Ningxia Hui Autonomous Region) (e.g. GU et al. 2010).

Family Bechalidae

Type (and only known) genus: *Bechala*

Diagnosis: Wing extremely narrow and long (ratio length/width: ~6.5), most probably broadest beyond mid-wing and, judging from the wing morphology close to the base, almost surely non-petiolate (plesiomorphy). Anterior margin concave at mid-wing. ScP– very short, close to costal margin, ending in costal margin proximally from mid-wing (autapomorphy). General pattern of main veins plesiomorphic. Stems of R and proximal part of RP– close to stem of M and MA+, but not coalesced. Likewise stem of M close to CuA+, but not fused. Cross-veins numerous and—compared to related families (vide infra)—rather irregularly arranged (plesiomorphy). Smooth remains of archedictyon present (strong plesiomorphy).

Remarks: Mesothoracic and metathoracic wings cannot be differentiated. Certainly they were nearly homonomous as in other early Megasecoptera.

Discussion

The Bechalidae share the non-petiolate wing shape and the plesiomorphic venation with a number of other families: (i) Brodiopteridae CARPENTER, 1963, (ii) Xenopteridae PINTO, 1986, (iii) Aspidothoracidae HANDLIRSCH, 1919 (all: Late Carboniferous), (iv) Bardohymenidae G. ZALESSKY, 1937 (Late Carboniferous to Early Permian), (v) Aykhalidae SINITSHENKOVA, 1994 (Carboniferous/Permian transition), and (vi) Alectoneuridae KUKALOVÁ-PECK, 1975 (Early Permian). All of them differ in their distinctly broader wing shape (see Table 4 for Arcioneuridae, Aspidothoracidae and Bardohymenidae) and the lack of remains of the archedictyon. Additionally, there are mainly the following distinguishing characters: (i) The Brodiopteridae differ by much longer ScP–, only few cross-veins, and lacking apical color marking; (ii) the Xenopteridae by much longer ScP–, smaller number of more regularly arranged cross-veins, and lacking apical color marking; (iii) the Aspidothoracidae by extremely longer ScP–, smaller number of more regularly arranged and often slightly sigmoidal cross-veins, and probably lacking apical color marking; (iv) the Bardohymenidae by longer and extremely weak ScP– freely ending between costal margin and RA+, as well as smaller number of more regularly arranged cross-veins; (v) the Aykhalidae by longer ScP–, smaller number of more regularly arranged cross-veins, and lacking apical color marking; (vi) the Alectoneuridae by basally tapering wing shape, and ScP– running close to RA+.

The Arcioneuridae KUKALOVÁ-PECK, 1975 have comparably long and slender wings with a length/width ratio of about 7.0 but differ distinctly in their petiolate wing base. From all other families of Megasecoptera the Bechalidae can be separated by their specific combination of characters: (i) archedictyon present (strongly plesiomorphic), (ii) wing extremely long and narrow but non-petiolate, with a length/width ratio of about 6.5, (iii) stems of R, M and CuA+ very close but never coalescent, (iv) apical color marking.

Genus *Bechala*

Etymology: In honor of the private collector H. Bech (Fröndenberg) and Latin “ala” for wing.

Type (and only known) species: *Bechala sommeri*

Diagnosis: As for the family.

Bechala sommeri

Fig. 27a–d, 28a; Tab. 4

Etymology: In honor of the preparator and private collector G. Sommer (Schleusingen).

Holotype: Left wing with preserved apical third and parts of the basal third, but lacking anterior margin, most parts of mid-wing and basis (AKH 524 a [negative print] and b [positive print]).

Paratype: Left wing with preserved apical quarter and parts of the basal third, but lacking of mid-wing and basis (AKS 458 a [positive print] and b [negative print]), Figs. 5c–d.

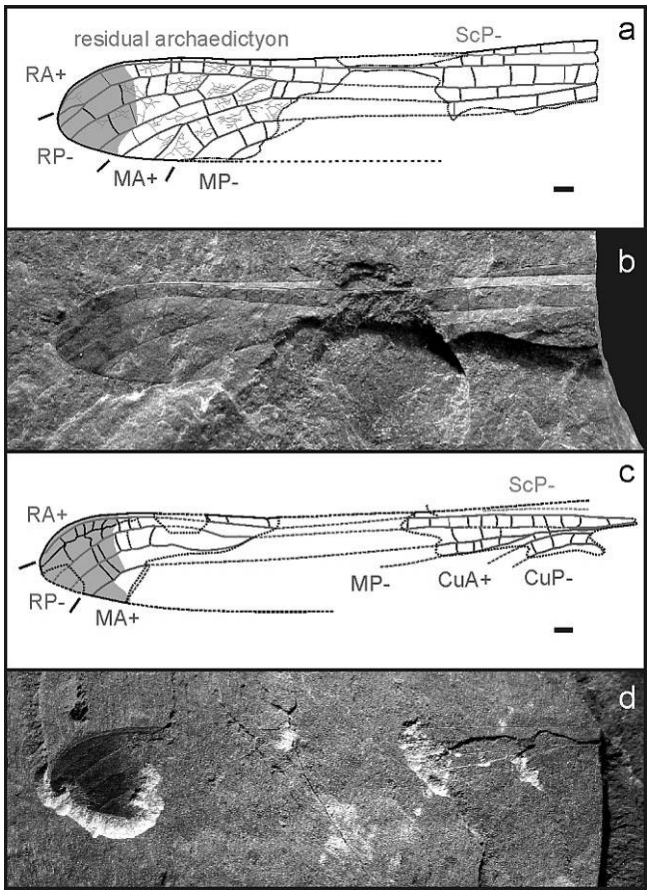


Fig. 27: *Bechala sommeri* (Bechalidae), late Namurian, Küchenberg quarry. **(a)–(b)** Holotype, specimen AKH 524. **(a)** Superimposed interpretative drawing, combined from positive and negative print, corrugation well visible, note the presence of both an archaedictyon and crossveins. **(b)** Photograph of positive print, colored apex clearly visible. **(c)–(d)** Paratype, specimen AKS 458. **(c)** Superimposed interpretative drawing, combined from positive and negative print. **(d)** Photograph of positive print, colored apex clearly visible, basal part hardly visible. Scale bars: 1 mm.

Type locality: Küchenberg near Fröndenberg, North Rhine-Westphalia, Germany (topographic map 4512 Menden; UTM coordinates (32U): N51°28.802, E007°44.429, topographic height ~160 m a.s.l.).

Type stratum: Late Carboniferous: latest Namurian B or C, probably Sprockhövel-Schichten (for further stratigraphical remarks see chapter 7.2). According to the Stratigraphic Table of Germany 2002 (DEUTSCHE STRATIGRAPHISCHE KOMMISSION 2002) the chronostratigraphic age is ~316.5–317.5 m.y.

Diagnosis: As for family (due to the temporarily monospecific status). Additional characters: Estimated length of wing ≤39.0 mm, but most probably not petiolate. Subcostal area near the wing base relatively broad. Apical area with distinct color marking.

Tab. 4: Measurements of wings in Megasecoptera probably close related to *Bechala sommeri*. FW: forewing; HW: hindwing; l: length [mm]; w: width [mm]; l/w: ratio length/width [-]. Annotation: * Variability of left and right forewing (probably due to preservation).

Taxon	l	w	l/w
Bechalidae			
Bechala sommeri; holotype	~39	~6	6.5
Bechala sommeri; paratype	~39	~6	6.5
Arcioneuridae Kukalová-Peck, 1975			
Arcioneura juvenilis Kukalová-Peck, 1975	18.5	2.6	7.1
Arcioneura havlatai Kukalová-Peck, 1975	40	5.7	7.0
Aspidothoracidae Handlirsch, 1919			
Aspidothorax triangularis Brongiart, 1894; FW	31	8	3.9
Aspidothorax triangularis Brongiart, 1894; HW	~20–35*	~8–8.5*	~3.3
Bardohymendiae G. Zalessky, 1937			
Alexahymen maruska Kukalová-Peck, 1972; FW	23	8.7	2.6
Alexahymen maruska Kukalová-Peck, 1972; HW	~30–31.8*	~9–9.9*	~3.3
Calohymen permianus Carpenter, 1947	25	6.5	3.8
Sylvohymen peckae Brauckmann, 1988	~15	~4.4	3.4
Sylvohymen pintoi Brauckmann et al., 2003; FW	~30	7	4.3
Sylvohymen sibiricus Kukalová-Peck, 1972; FW	50	9.1	5.5

Preservation: Both wings are rather well preserved with clearly visible venation and apical color marking. At least in the paratype, even the corrugation is recognizable although it seems to be flattened by diagenesis and tectonics. In both the holotype and the paratype the basal quarter of the wing is broken off, and thus the articulation area is missing; furthermore the posterior margin is not recognizable over a long distance. The mid-wing area is not preserved in the paratype and poorly visible in the holotype. Only visible in the holotype, the apical part of the wing exhibits remains of an archedictyon between main veins and coexisting cross-veins. This

meshwork of very thin veinlets is hardly visible (Fig. 28a). Due to its appearance and configuration we exclude that it is the result of secondary processes like diagenetic shrinking cracks, preparation or storage damages. We rather assume that the archedictyon was very thin and capillary in *B. sommeri* and therefore is not well preserved in general. There is only evidence for veinlets of an archedictyon in the distal third of the wing length. This can either be due to preservation or to the archedictyon being restricted to this part of the wing—e.g. as a structural support during flight. It cannot be excluded that further preparation of the specimens would uncover additional features of the wing.

Measurements: Holotype (AKH 524): preserved length: 33.1 mm; estimated length: ≤39.0 mm; preserved width: 5.2 mm; estimated width: ~6.0 mm. Paratype (AKS 458): preserved length: 27.3 mm; estimated length: ≤39.0 mm; preserved width: 5.7 mm; estimated width: ~6.0 mm.

Description: Wing extremely narrow and broadest at mid-wing, non-petiolate, base most probably relatively broad. Pattern of main venation reduced. Anterior margin basally slightly convex, at mid-wing concave over a long distance, distally strongly convex towards apex. Apex shifted backwards. Subcostal area with a series of rather regular cross-veins. ScP– closer to costal margin than to RA+, very short, and ending in anterior margin near mid-wing. Forking of RA+ and RP– very close to wing base. RA+ simple, very close and subparallel to anterior margin in distal quarter, terminating very close to apex. RP– branching in distal quarter, with 2–4 terminal branches ending at and slightly behind apex. MA+ and MP– branching in the basal third, considerably proximally of RP– origin. MP– long, subparallel to MA+, with at least two terminal branches. Corrugation well developed. Apical color marking similar to *Sylvohymen peckae* and *S. pintoi* (family Bardohymenidae) but reaching terminal branches of MA+.

Discussion

Sylvohymen peckae and *S. pintoi* from Hagen-Vorhalle are most probably slightly older than *Bechala sommeri* from the Küchenberg with whom they share the conspicuous apical color marking. But the latter species exhibits additional extremely plesiomorphic characters, e.g. (i) the broad and non-petiolate wing base (distinctly indicated by the broad basal area of MP– and CuA+/CuP–), (ii) large number of rather irregularly arranged cross-veins, and (iii) smooth remains of an archedictyon between them. In our opinion the coexistence of an archediction and well developed cross-veins indicates that *B. sommeri* resembles a transient form of a lower evolutionary plateau within the Megasecoptera. Presumably there was a Palaeodictyoptera-like finely woven archedictyon present in the groundplan pattern of the group. Evolving from this original stage some veinlets of the archedictyon may be accented successively forming real cross-

veins. Concurrently intercalated veinlets were reduced. In this interpretation the species represents an intermediate stage bearing both strongly plesiomorphic features and apomorphic characters in combination. Similar conditions can be observed in *Erasipteron larischi* PRUVOST, 1933 (Odonatoptera MARTYNOV, 1923: "Erasipteridae"; Fig. 29b) and have been reported by BRAUCKMANN & ZESSIN (1989: fig. 24). The assumption that the archedictyon was already reduced to a number of capillary veinlets is supported by the fact that is can only be found in the holotype, where it is difficult to see. Despite the similarly well-preserved state of the paratype, the archedictyon is not at all visible in that specimen.

It cannot be excluded that other, already described, taxa of Megasecoptera may exhibit such an archedictyon, too. But due to its capillary thinness it may not be preserved—or recognized—in these specimens.

In general, the Bechalidae may represent a pattern of characters close to the groundplan of the Megasecoptera or even of the Palaeodictyoptera.

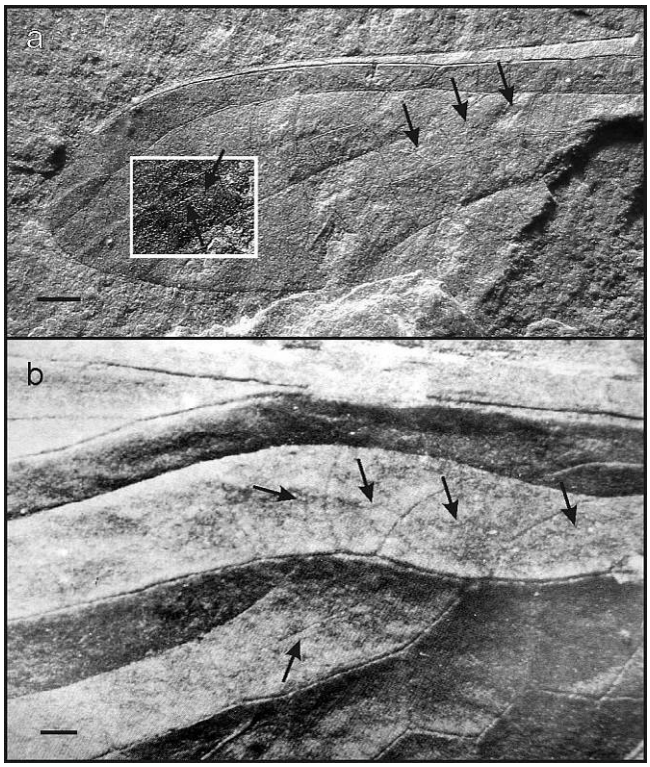


Fig. 28: Residual archedictyon in different taxa. **(a)** *Bechala sommeri* (Bechalidae), holotype (specimen AKH 524), late Namurian, Küchenberg quarry, photograph of the apical area. Arrows indicate some parts of the tiny and hardly visible archaedictyon; white box: detail of the venation pattern with digitally overemphasized contrast and illumination setting to accent fine meshwork of the archedictyon. **(b)** *Erasipteron larischi* PRUVOST, 1933 (Odonatoptera: "Erasipteridae"), holotype (MBI 455), Namurian C, Horní Suchá (Czech Republic), detail of the venation pattern in the area of CuP– and AA+ branching; arrows indicate the archedictyon; image adopted from BRAUCKMANN & ZESSIN (1989: fig. 24). Scale bars: 1 mm.

Infraclass: Neoptera MARTYNOV, 1923

Basal Neoptera

Genus *Kochopteron* BRAUCKMANN, 1984

Type and only known species: *Kochopteron hoffmannorum* BRAUCKMANN, 1984, late Namurian B; Hagen-Vorhalle, Germany.

Diagnosis: See BRAUCKMANN (1984); BRAUCKMANN et al. (2003).

***Kochopteron hoffmannorum* BRAUCKMANN, 1984**
Fig. 29

v* 1984 *Kochopteron hoffmannorum* BRAUCKMANN: 114, fig. 4.
v 1985 *Kochopteron hoffmannorum*. – BRAUCKMANN et al.: 74–76, figs. 56–57, pls. 21–22.
v 2003 *Kochopteron hoffmannorum*. – BRAUCKMANN et al.: 43–45, fig. 17, pls. 8–9.
v 2008 *Kochopteron hoffmannorum*. – ILGER & BRAUCKMANN: 279–285, figs. 1–2.

Holotype: Specimen no. WMf.N P. 22596, deposited in the collection of the LWL-Museum für Naturkunde in Münster. BRAUCKMANN & GRÖNING (1998: 80) still used its preliminary number ("H3") of the Hoffmann collection.

New material from the Küchenberg site: One isolated wing fragment, proximal half of right mesothoracic wing: AKH 1516 a (positive print) and b (negative print).

Diagnosis: See BRAUCKMANN (1984); ILGER & BRAUCKMANN (2008).

Measurements: Preserved length: ~15.3 mm, width: ~7.5 mm.

Preservation: The distal part is disrupted slightly before first forking of MP–. Corrugation and cross-veins are clearly visible. Contrary to most specimens from Hagen-Vorhalle, the entire anal area is rather well preserved.

Remarks: Mesothoracic wings are remarkably narrower than metathoracic wings and have a reduced anal area. Due to this character, the Küchenberg specimen can clearly be indentified as a mesothoracic wing.

Discussion: Both in size and shape the Küchenberg wing fits very well within the range of other known specimens of *K. hoffmannorum*. The presence of an arculus (= cross-vein between MP– and CuA+ in the basal quarter of the wing) indicates the affiliation to "basal Neoptera".

Since the distal part is lacking, it is not clear if ScP– ends in the costal margin or in RA+. This is a main character for the separation from *Holasicia rasnitsyni* (family Paoliidae). But the cross-venation in the preserved area between costal margin and basal ScP– is typically pectinate in *K. hoffmannorum* as preserved in the present specimen. Contrarily, and unlike in the Küchenberg specimen, in *H. rasnitsyni* the cross-veins form a fine archedictyon-like network in this area. Obviously the Küchenberg specimen seems to be slightly more elongated than those ones from Hagen-Vorhalle which may be caused by tectonic deformation and/or preservation.

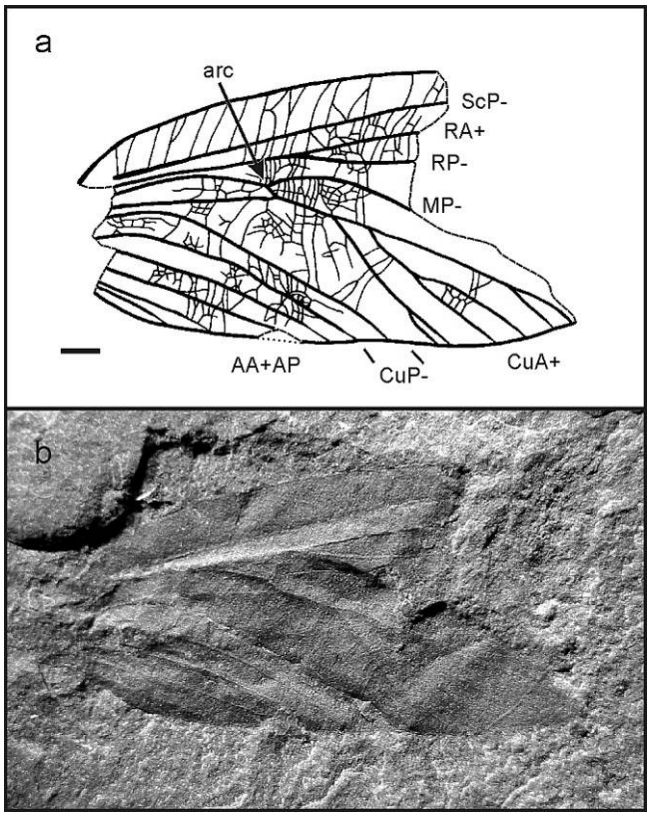


Fig. 29: *Kochopteron hoffmannorum* BRAUCKMANN, 1984, specimen AKG 1516, late Namurian, Küchenberg quarry, right mesothoracic wing. **(a)** Superimposed interpretative drawing, combined from positive and negative print, scale: 1 mm. **(b)** Positive print, photograph in polarized light.